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METABOLISM AND PHYSIOLOGY OF DOUBLE MUSCLED CATTLE

by

© ROBERT A. STRATH

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH

IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE

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IN

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ABSTRACT

A series of investigations was conducted to study the metabolic and physiological responses of double muscled (DM) cattle to mild stressors and to study some aspects of reproduction in this cattle type.

In the first study (Chapter II) the effects of a 4 d fast and a 3 d heat exposure were studied in three extreme muscled (DM) and three of their normal-to-moderate muscled (carrier) half-siblings. In both animal types plasma free fatty acid concentrations more than doubled ($p<0.01$) during fasting, although concentrations in DM animals were lower than those in carrier animals ($p<0.05$). During the fast, blood urea nitrogen concentration decreased in the carrier cattle and increased in the DM animals ($p<0.05$). The mean rectal temperature of the carriers remained constant during the heat exposure, while that of the DM bulls was elevated ($p<0.05$). The respiratory frequency was elevated ($p<0.01$) for both animal types after the heat exposure and this increased frequency was higher ($p<0.05$) for DM bulls than carrier bulls. A significant ($p<0.05$) decrease in triiodothyronine (T_3) concentration appears to be characteristic response of DM cattle to both a fast and heat exposure.

In the second study (Chapter III) plasma glucose kinetics were determined in the same animals in both the fed state and after a 4 d fast. There were no statistically significant effects observed for plasma glucose or blood

lactic acid concentrations. Total entry rate (TER) and irreversible loss (IRL) of plasma glucose were both lower ($p<0.05$) in the fasted state for both animal types. Glucose pool size tended to be smaller ($p<0.1$) in the fasted state and was observed to be smaller ($p<0.05$) in the DM compared with the carrier bulls.

In the third study (Chapter IV) serum T_3 kinetics were determined in the same animals when fed grass hay ad libitum and metabolic rate was estimated for a 24 h period in four DM and four carrier bulls starting 12 h after feed was removed. Pool size of T_3 was higher ($p<0.001$) in the DM cattle and no significant effects were observed for TER. The IRL of T_3 tended ($p<0.1$) to be higher in the DM animals. Metabolic rate was higher ($p<0.05$) for the DM cattle compared with the carrier cattle. These results indicate that DM cattle may be relatively hyperthyroid compared with carrier animals.

In the fourth study (Chapter V) the reproductive capabilities of a small DM herd were studied. DM heifers do not generally ($p<0.001$) have live calves as a result of their first breeding season. The estrous cycle of three DM cows was apparently normal as indicated by plasma estradiol-17β, luteinizing hormone and progesterone concentration patterns and by behavioural events at estrus.

In the fifth study (Chapter VI) the response of DM and carrier cattle to halothane anaesthesia was studied. Neither skeletal muscle tremors nor muscle rigidity were observed in

DM cattle after a 30 min period of stage III plane 2 anaesthesia maintained by halothane, while heart rate was elevated ($p<0.001$) as a result of the anaesthetic. There were no signs of halothane sensitivity as indicated by rectal temperature, arterial pH, nor by venous lactic acid, adrenaline and noradrenaline concentrations in a young DM calf exposed to halothane.

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I. GENERAL INTRODUCTION TO DOUBLE MUSCLING IN CATTLE

A. Introduction

The double muscled (DM) syndrome is a genetic condition in beef cattle which is characterized by a generalized skeletal muscular hypertrophy (Ansay and Hanset 1979). Affected animals have enlarged forelimb, thigh and neck muscles plus a well rounded rump when viewed laterally. Visually the enlarged muscles of DM cattle are made more prominent by thinner hides and reduced subcutaneous fat thickness (Oliver and Cartwright 1968). Cattle breeders are selecting for animals which are lean and muscular as they are more efficient producers of a high quality edible product. In addition, meat from these carcasses contains less fat making them more appealing to consumers. Since DM cattle appear to be a superior "meat" type animal, attention is focusing on the DM syndrome.

The first description of the DM syndrome by Cully in 1807 (cited by Oliver and Cartwright 1968) indicated that DM cattle were considered "monsters" and that carcasses obtained from these cattle were free of fat and were dark. Oliver and Cartwright (1968) traced the origin of DM cattle from Holland to England where they were introduced into the genetic pools of numerous present day European breeds. The term "double muscled" was first reported by Weber and Ibsen in 1934 (cited by Kieffer and Cartwright 1980) to describe some Herefords within a purebred herd in Nebraska. The term

double muscled is a misnomer, for affected animals have the identical number of muscles as normal cattle (Oliver and Cartwright 1968). Since "double muscling" and "double muscled" are commonly used terms for describing this cattle type in North America, Australia, Britain and some European countries they will be used throughout this thesis. Some authors prefer to use hereditary muscular hypertrophy, muscular hypertrophy or MH to describe this cattle type due to the generalized enlargement of the skeletal muscles, but other tissues and organs are also affected. Therefore the use of muscular hypertrophy to describe this cattle type is not the most correct term. Until this abnormality of cattle can be explained in exact genetic terms the use of the term "double muscling" is recommended for it describes the animals and implies minimal scientific or clinical significance to both producers and animal scientists.

Double muscled cattle have some similarities to stress susceptible (SS) swine. Both of these animal types have enlarged muscles, reduced body fat and are more stress susceptible as compared with normal animals of their species (Ashmore 1974). Furthermore, relatively fragile erythrocytes have been reported in both SS swine (Cheah and Cheah 1979) and DM cattle (Basarab et al. 1980). Halothane, a fluorinated hydrocarbon anaesthetic, causes a condition known as malignant hyperthermia in SS swine (Britt 1972). A reliable test for identifing SS pigs is to expose a young pig to halothane for a few minutes. The development of

muscular rigidity indicates that the animal is stress susceptible (Eikelenboon and Minkema 1974).

There is considerable research reported on double muscling in cattle, but it should be emphasized that there are many limitations to extrapolating the results of one study to another. Experimenters have compared DM cattle with control cattle, but in many instances they have not indicated the genotype of the control animals, which could have been either "normal" or "carrier" cattle. Many of the experiments reported in the literature dealing with the DM syndrome in cattle have involved animal numbers as small as one per group and have occasionally varied in factors such as age and sex between treatment groups. The DM syndrome has been reported to occur in most European breeds of cattle. The DM syndrome in a breed may be modified by its characteristic breed phenotype to the extent that the expression of the syndrome may differ within the various cattle breeds. Similarly, many production and experimental DM herds have different selection pressures exerted on them for traits such as muscling, growth rate, and reproductive performance so that the phenotypic expression of the DM syndrome varies between herds.

There are a number of reviews of the scientific literature concerning double muscling in cattle (Bradley 1978; Heine and Neumann 1977; Kieffer and Cartwright 1980; Menissier 1974; Oliver and Cartwright 1968; Vandeplassche 1974) which the reader is referred to for a detailed

description of the DM syndrome. The purpose of the present review is to introduce the double muscled syndrome to the reader, to discuss its inheritance and to identify the major advantages and disadvantages of this animal type in cattle production.

B. Physical Characteristics and Body Composition of DM Cattle

Kieffer and Cartwright (1980), Menissier (1974), Oliver and Cartwright (1968) and West (1974) describe the gross anatomical characteristics of DM cattle in detail. Phenotypically DM cattle are easy to identify by the gross enlargement of the skeletal musculature and by the characteristic creases between the muscles of the hindquarters (Rollins et al. 1972). These intermuscular grooves are due to the enlarged muscles and are accentuated by thinner hides and reduced subcutaneous fat thickness (Oliver and Cartwright 1968). Generally, muscular hypertrophy occurs in most of the skeletal muscles but particularly in those involved with locomotion (Ansay and Hanset 1979). Johnson (1981) has reported muscular hypertrophy of the larger superficial skeletal muscles, whereas the muscles located deeper within the DM animal exhibited only minor hypertrophy. Exceptions to the generalized hypertrophy are the intercostal and abdominal muscles which are proportionately smaller in DM cattle, probably because the lungs and digestive tract of this

cattle type are smaller than normal cattle of similar body weight (Boccard and Dumont 1974). Other physical characteristics described by Kieffer and Cartwright (1980) include bowed front legs, fineness of the limb bones, forward attachment of a short tail, underdeveloped external genitalia, a stretched appearance when standing and open shoulders. Kieffer and Cartwright (1980) have reported that enlarged tongues of newborn calves are common and Hanset and Michaux (1978) have observed a minor deformity in the mandible in some DM animals of the Belgian Blue and White breed. Cattle which are heterozygous for the double muscled traits are called carriers and usually show an intermediate phenotype between DM and normal muscled cattle within a given breed (Kieffer and Cartwright 1980).

Limb bones of DM cattle are smaller in diameter than those of comparable normal animals (Oliver and Cartwright 1968) This feature is accentuated by the large muscle mass over the shoulders and hindquarters of the animals. The long bones of DM animals are lighter than those from normal muscled animals of similar weight within the Belgian Blue and White breed (Ansay and Hanset 1979). Hendricks et al. (1973) reported that DM bulls had shorter metacarpals which have thinner cortices than either carrier or normal muscled bulls. Rollins et al. (1980) surveyed the literature and reported that DM cattle have an average muscle to bone ratio 60% greater than normal muscled animals.

The total amount of body fat is substantially below normal in DM cattle (Oliver and Cartwright 1968). All major fat depots such as the subcutaneous, renal, pelvic and intermuscular depots are reduced. A survey of dissection studies by Rollins et al. (1980) revealed that the fat to bone ratio was on average 26% smaller for DM cattle compared with normal muscled cattle.

Other tissues besides muscle, bone and fat are present in different proportions in DM cattle than in normal cattle. Internal organs such as the thymus, spleen, lungs, kidney, liver, digestive tract and heart are all significantly smaller in DM cattle when expressed on a total body weight basis (Ansay and Hanset 1979). Skeletal muscle is the only major tissue which is known to undergo hypertrophy in DM cattle, whereas most other tissues are proportionately smaller, resulting in an increased quantity of lean meat obtained from the carcasses of DM cattle. In some European countries where lean meat commands a premium price, the production disadvantages in raising DM cattle are overshadowed, to the extent that DM cattle production is very profitable (Hanset and Leroy 1979).

Other characteristics of DM cattle include relatively fragile erythrocytes (King et al. 1976; Basarab et al. 1980) which have been suggested to be indicative of a generalized cell membrane defect (King 1975). The thyroid hormone triiodothyronine concentration was observed to be both higher (Basarab 1981) and lower (Novakofski and Kauffman

1981) in DM cattle compared to normal muscled cattle. Basarab (1981) has observed an altered fatty acid compositon of some of the phospholipid fractions of the erythrocyte plasma membrane in DM cattle. Erythrocyte glucose consumption and lactic acid production have also been shown to be greater in DM cattle as compared with normal cattle (Basarab 1981). Some plasma enzymes have been reported to have a different activity pattern in DM cattle (Kolataj et al. 1979a b; Konecka et al. 1979) which may reflect a generalized cell membrane defect.

C. Advantages of DM Cattle

The major advantage of DM cattle is the increased yield of lean meat. A brief discussion of growth and development, muscle fiber types and innervation of the skeletal muscles of DM cattle is necessary to understand why more meat, which is primarily composed of muscle tissue, is obtained from carcasses of this cattle type.

Double muscling is a genetic condition of cattle which can be detected early in fetal development of an animal. Swatland and Kieffer (1974) reported a generalized muscular hypertrophy in locomotory muscles of DM fetuses. Histological evidence suggests that the muscle enlargement of DM fetuses is primarily a result of hyperplasia (Swatland and Kieffer 1974). Ansay (1976), in a detailed dissection study observed that DM fetuses at a given crown-rump length had 26 to 64% more skeletal muscle than normal muscled

fetuses. Similarly, Ashmore et al. (1974) observed that the muscles of DM fetuses were larger due to an increased number of α-muscle fibers. Research by N.M. Kieffer from Texas A&M University (cited by Anonymous 1978) has suggested that the developmental control of the DM syndrome in the fetus may be due to a blood-borne gene product. To determine the exact biochemical etiology of double muscling it may be necessary to study the condition in utero.

Considerable research on muscle fiber typing of the enlarged muscles of DM cattle has been reported (Ashmore and Robinson 1969; Holmes and Ashmore 1972; Hendricks et al. 1973; Swatland 1973; Ashmore et al. 1974; Mascarello and Geroldi 1974; Swatland and Kieffer 1974). All authors have concluded that the muscular hypertrophy of DM cattle is primarily a result of hyperplasia of the α-white muscle fibers. Ashmore (1974) has indicated that muscle fiber types can greatly influence the quality of meat obtained from a carcass. Excess pre-slaugher stress to DM cattle can result in poor quality meat, such as dark cutting, from carcasses of this cattle type (Ashmore 1974).

Swatland and Cassens (1974) have emphasized that the innervation of skeletal muscles in domestic animals is important in determining the quality and quantity of the meat obtained from a given animal type. Swatland (1973) observed an increased number of branched terminal axons in the enlarged muscles of DM cattle compared to muscles of normal cattle. Recently, Novakofski et al. (1981) attempted

to identify heterozygotes for double·muscling by determining the number of axonal branches in muscles obtained from DM, carrier and normal muscled cattle. Their results indicated a large variation and overlap between genotypes and they concluded that determining the functional terminal innervation ratio was of minimal value in identifing the genotype of an animal.

The double muscled syndrome offers many advantageous characteristics for meat production. Oliver and Cartwright (1968) have reported that DM cattle have a higher dressing percentage due to the increased muscle tissue, reduced amount of body fat, lighter bones, smaller internal organs and thinner hides. Hanset et al. (1980) have recently reported that DM bulls from 215 to 370 days of age have a significantly superior feed conversion efficiency compared to normal muscled cattle of similar breeding. Boccard and Dumont (1974) have reported that the connective tissue within the enlarged muscles of DM cattle is less than that in normal muscled cattle. The extent of development of the perimysium in the hypertrophied muscles of DM cattle is less than that of conventional beef cattle (Dumont and Schmitt 1973). The meat obtained from cattle possessing the double muscled trait has been reported to be equal (Carroll et al. 1978) or superior (Bouton et al. 1978) in tenderness to meat obtained from normal muscled cattle. Considering the above, it would appear that DM cattle are a superior "meat" producing animal type.

D. Disadvantages of DM Cattle

There are some serious disadvantages associated with DM cattle which limit their apparent value to livestock production. Cattle displaying the DM syndrome are more susceptible to various stressors and have a poor reproductive capability (Kieffer and Cartwright 1980).

Holmes et al. (1972b) have reported that DM cattle are more temperamental, possibly because of the accumulation of excessive amounts of lactic acid during states of severe stress. For example, they reported that after an exercise stress, a DM heifer collapsed and developed myoglobulinuria due to excess lactic acid build up (Holmes et al. 1972a). Monin and Boccard (1974) observed that DM animals often exhibited metabolic acidosis during exercise, and partially attributed the condition to a reduced capacity of oxidative metabolism arising from the proportionally smaller heart and lungs plus the lower hematocrit of this cattle type. Similarly, Holmes et al. (1973) observed that the combination of bleeding and fasting was more stressful for DM cattle than for normal cattle as indicated by blood metabolite and post-slaughter muscle pH measurements. Halipre (1973) has observed that DM cattle are more susceptible to an acute heat stress as compared with normal cattle. Holmes and Robinson (1970) have reported that DM cattle are prone to losing considerable muscling when fed a diet below maintenance energy. The University of Alberta maintains a small herd of DM cattle and several of the most

muscular cattle in this herd have died suddenly, and upon post mortem examination no specific cause of death has been indicated. Cattle within this herd have also been observed to lose considerably more body condition over severe winters than do their normal muscled contemporaries.

The major disadvantage associated with DM cattle production is the poor reproductive performance of the females (Oliver and Cartwright 1968). Vissac et al. (1974) have shown that puberty may be delayed, milk production is reduced and abnormal estrous cycles occur more often in DM than in normal cows. Dystocia, stillbirths and caesarian sections are relatively common in DM cows (Kieffer and Cartwright 1980). Hanset and Jandrain (1979) have reported that more than 48% of the DM heifers and 25% of the DM cows in the Belgian Blue and White breed require caesarian section. Menissier et al. (1974) have suggested that the poor fertility of DM cows may be attributed to a defective sexual behaviour at estrus, possibly arising from an endocrine disturbance.

The enlarged tongue of neonatal DM calves makes sucking difficult (Oliver and Cartwright 1968) and the reduced amount of milk produced by DM dams (Vissac et al. 1974) both contribute to poor viability of the calves. Hanset and Jandrain (1979) have indicated that the selection for double muscling has resulted in poor viability of the young DM calf.

Most authors in North America (Oliver and Cartwright 1968; Holmes et al. 1973; Ashmore 1974; Kieffer and Cartwright 1980) have indicated that the increased production of lean meat from DM cattle does not compensate for the increased economic losses arising from increased stress susceptibility, decreased reproduction capabilities or the reduced viability of DM calves. In Europe, the veterinarian plays a key role in meat production from DM cattle (Hanset 1979), which is presently economical due to the high premium paid for DM carcasses (Hanset and Leroy 1979).

E. Genetics and Implications of the DM Syndrome

There is some disagreement about the mode of inheritance of the DM syndrome in cattle. Due to the variable phenotypic expression of the condition in the heterozygote or carrier, it has not always been possible to identify the genotype of an animal (Oliver and Cartwright 1968). Most authors (Oliver and Cartwright 1968; Rollins et al. 1972; McKellar and Ouhayoun 1973; Hanset 1974; Nott and Rollins 1979; Kieffer and Cartwright 1980; Basarab 1981) have indicated that the DM syndrome is inherited as a single recessive gene pair with incomplete penetrance.

Carrier cattle, which are phenotypically intermediate between normal muscled and DM cattle, do not appear to have the production problems associated with the double muscling trait (Kieffer and Cartwright 1980) yet have superior

carcasses (Rollins et al. 1980) and meat quality (Bouton et al. 1978) as compared with normal cattle. Many authors (Hanset 1975; Hanset and Leroy 1979; Rollins et al. 1980) have suggested that the DM trait may be exploited in the heterozygote to take advantage of the superior growth and carcass value of the carrier, as compared with normal muscled cattle, while minimizing the production disadvantages associated with DM cattle.

F. Summary

The double muscled syndrome in cattle is inherited as a recessive trait with incomplete penetrance. Affected animals have enlarged skeletal muscles due to an increased number of muscle fibers. The major fat depots and the limb bones of DM cattle are smaller than normal muscled cattle. Some DM cattle populations have an increased rate of growth and superior feed conversion efficiency up until one year of age. Meat from DM carcasses is of high quality for the amount of connective tissue in the skeletal muscles is reduced, resulting in relatively more tender meat.

Stress susceptibility, poor viability of young DM calves and the poor reproductive capabilities of DM females limit the usefulness of this cattle type. These disadvantages of utilizing DM cattle in beef production are reduced in the heterozygote animals while meat yield remains superior to normal cattle. Thus producers have recently been encouraged to raise this intermediate phenotype as market

animals.

G. Thesis Objectives

The major disadvantages of utilizing DM cattle in livestock production are the increased stress susceptibility and the poor reproductive performance of this cattle type. A series of experiments were undertaken to study the effects of mild stressors on the metabolism and physiology of DM cattle (Chapter II and III). The object of Chapter IV was to determine whether the thyroid status of DM cattle differs from normal muscled cattle. A trial was conducted to identify some of the possible causes of the poor reproductive capability of DM cattle (Chapter V). Finally a study was performed to study the response of DM cattle to the common anaesthetic halothane (Chapter VI).

H. References

ANONYMOUS, 1978. Genetic engineering in cattle offers exciting possibilities. Better Beef Business, October 1978: 6-7.

ANSAY, M. 1976. Development anatomique du muscle de foetus bovin. Etude particuliere de l'effect "culard". Ann. Biol. anim. Bioch. Biophys. 16: 655-673.

ANSAY, M. and HANSET. R. 1979. Anatomical, physiological and biochemical differences between conventional and double-muscled cattle in the Belgian Blue and White breed. Livest. Prod. Sci. 6: 5-13.

ASHMORE, C. R. and ROBINSON, D. W. 1969. Hereditary muscular hypertrophy in the bovine: I. Histological and biochemical characterization. Proc. Soc. Exp. Biol. Med. 132: 548-554.

ASHMORE, C.R. 1974. Phenotypic expression of muscle fiber types and some implications to meat quality. J. Anim. Sci. 38: 1158-1164.

ASHMORE, C.R., PARKER, W., STOKES, H. and DOERR, L. 1974. Comparative aspects of muscle fiber types in fetuses of the normal and "double muscled" cattle. Growth 38: 501-506.

BASARAB, J.A. 1981. Genetic and physiological characterization of the double muscled syndrome in cattle. PhD Thesis, The University of Alberta.

BASARAB, J.A., BERG, R.T. and THOMPSON, J.R. 1980. Erythrocyte fragility in "double-muscled" cattle. Can. J. Anim. Sci. 60: 869-879.

BOCCARD, R. and DUMONT, B.L. 1974. Consequences de l'hypertrophie musculaire hereditaire des bovins sur la musculature. Ann. Genet. Sel. anim. 6: 177-186.

BOUTON, P.E., HARRIS, P.V. and SHORTHOSE, W.R. 1978.

Comparison of some properties of meat from normal steers and steers heterozygous for muscular hypertrophy. Meat Sci. 2: 161-167.

BRADLEY, R. 1978. Double-muscling in cattle--boon or bane? Veterinary Annual 18: 51-59.

BRITT, B.A. 1972. Recent advances in malignant hyperthermia. Anesth. Analg. 51: 841-850.

CARROLL, F.D., THIESSEN, R.B., ROLLINS, W.C. and POWERS, N.C. 1978. Comparison of beef from normal cattle and heterozygous cattle for muscular hypertrophy. J. Anim. Sci. 46: 1201-1205.

CHEAH, K.S. and CHEAH, A.M. 1979. Mitochondrial calcium, erythrocyte fragility and porcine malignant hyperthermia. FEBS Letters 107: 265-268.

DUMONT,B.L. and SCHMITT, O. 1973. Consequences de l'hypertrophie musculaire hereditaire sur la trame conjonctive du muscle de bovin. Ann. Genet. Sel. anim. 5: 499-506.

EIKELENBOOM, G. and MINKEMA, D. 1974. Prediction of pale, soft, exudative muscle with a non-lethal test for the halothane-induced porcine malignant hyperthermia syndrome. Tijdschr. Diergeneesk. 99: 421-426.

HALIPRE. A. 1973. Etude du caractere culard. X--Sensibilite des bovins culards au stress thermique. Ann. Genet. Sel. anim. 5: 441-449.

HANSET, R. 1974. Modeles de selection en faveur d'un gene: Application au cas du gene "culard", en race Blanc Blue Belge. An. Med. Vet. 118: 507-518.

HANSET, R. 1975. L'exploitation du gene "culard", en croisements. La determination de l'importance relative des differents compartiments dans les schemas de croisements. Ann. Med. Vet. 119: 1-10.

HANSET, R. 1979. L'amelioration genetique du cheptel bovin et le veterinaire. Ann. Med. Ved. 123: 5-16.

HANSET, R. and JANDRAIN, M. 1979. Selection for double-muscling and calving difficulties. In: *Calving problems and early viability of the calf*. Edited by B. Hoffmann, I.L. Mason and J. Schmidt. Martinus Nijhoff Publishers; The Hague, Boston, London. pp 92-104.

HANSET, R. and LEROY, P. 1979. Variatons du revenu brut dans un troupeau de bovins a viande du type hypermuscle. Etude par simulation. Ann. Med. Vet. 123: 263-274.

HANSET, R. and MICHAUX, C. 1978. Anomalies au niveau du maxillaire inferieur (brachygnathisme et deviation) chez le bovin culard. Ann. Med. Vet. 122: 649-655.

HANSET, R., STASSE, A. and MICHAUX, C. 1979. Feed intake and feed efficiency in double-muscled and conventional cattle. Z. Tierzuchtg. Zuchtgsbiol. 96: 260-269.

HEINE, C. and NEUMANN, A. 1977. Die doppellendigkeit beim rind-- Geschichte, vertbeitung, problem und anwendbarkeit. Arch. Tierzucht. 6: 405-418.

HENDRICKS, H.B., ABERLE, E.D., JONES, D.J. and MARTIN, T.G. 1973. Muscle fiber type, rigor development and bone strength in double muscled cattle. J. Anim. Sci. 37: 1305-1311.

HOLMES, J.H.G. and ASHMORE, C.R. 1972. A histochemical study of development of muscle fiber type and size in normal and "double muscled" cattle. Growth 36: 351-372.

HOLMES, J.H.G., ASHMORE, C.R. and ROBINSON, D.W. 1973. Effects of stress on cattle with hereditary muscular hypertrophy. J. Anim. Sci. 36: 684-694.

HOLMES, J.H.G., ASHMORE, C.R., ROBINSON, D.W., FINN, J.P.and O'DELL, J. 1972a. A condition resembling "Azoturia" in a "Double Muscled" heifer. Vet. Rec. 90: 625-630.

HOLMES, J.H.G. and ROBINSON, D.W. 1970. Hereditary muscular hypertrophy in the bovine: metabolic response to nutritional stress. J. Anim. Sci. 31: 776-780.

HOLMES, J.H.G., ROBINSON, D.W. and ASHMORE, C.R. 1972b.

Blood lactic acid and behaviour in cattle with hereditary muscular hypertrophy. J. Anim. Sci 35: 1011-1013.

JOHNSON, E.R. 1981. Carcass composition of double-muscled cattle. Anim. Prod. 33: 31-38.

KIEFFER, N.M. and CARTWRIGHT, T.C. 1980. Double muscling in cattle. Tech. Rep. No. B-1325. The Texas Agricultural Experimental Station. Texas A&M University System, College Station. pp 33-43.

KING, W.A. 1975. Herediatary muscular hypertrophy (double muscling) in beef cattle. MSc Thesis, University of Guelph.

KING, W.A., BASRUR, P.K., BROWN, R.G. and BERG, R.T. 1976. Osmotic response tests on erythrocytes for the detection of double muscled carriers in cattle. Ann. Genet. Sel. anim. 8: 41-45.

KOLATAJ, A., REKLEWSKI, Z., DEMBOWSKI, J., TYRAWSKA-SPYCHALOWA, D. and DZIEWIECKI, C. 1979. Physiological aspects of muscular hypertrophy in cattle. I. Activity of some enzymes in blood plasma. Z. Tierzuchtg. Zuchtgsbiol. 95: 222-226.

KOLATAJ, A.,SWIERGIEL, A.H., DZIEWIECKI, C. and KONECKA, A.M. 1979. Physiological aspects of muscular hypertrophy in cattle. III. Activity of ICDH, MDH and cholinesterase in blood plasma. Z. Tierzuchtg. Zuchtgsbiol. 96: 186-190.

KONECHA, A.M., KOLATAJ, A., DZIEWIECKI, C. and SWIERGIEL, A. 1979. Physiological aspects of muscular hypertrophy in cattle. II. The activity of LDH and levels of L-lactic acid and glucose in the blood plasma. Z. Tierzuchtg. Zuchtgsbiol. 95: 227-231.

MASCARELLO, F. and GEROLDI, R. 1974. Tipizzazione delle fibre muscolari in bovine Piedmontesi "della coscia". Atti. Soc. It. Sc. Vet. 28: 458-460.

MCKELLAR, J.C. and OUHAYOUN, J. 1973. Etude du caractere culard. VIII. Frequency et expression en race South

Devon. Ann. Genet. Sel. anim. 5: 163-176.

MENISSIER, F. 1974. Hypertrophie musculaire d'origine genetique chez les bovins: description, transmission, emploi pour l'amelioration de la production de viande. In: *First World Congress on Genetics Applied to Livestock Production*.Madrid, Spain. 85-107.

MENISSIER, F., CHUPIN, D., CHEMINANT, E., FABRE, F. and FABRE, G.P. 1974. Fertilite induite sensibilite a la P.M.S.G. de femellles culardes. In: *First World Congress on Genetics Applied to Livestock Production*. Madrid, Spain. pp 81-98.

MONIN, G. and BOCCARD, R. 1974. Caracteristiques physiologiques respiratoires des bovins culards. Ann. Genet. Sel. anim. 6: 187-193

NOVAKOFSKI, J.E. and KAUFFMAN, R.G. 1981. Biological detection of heterozygosity for double muscling in cattle. II. Thyroid hormone concentrations. J. Anim. Sci. 52: 1437-1441.

NOVAKOFSKI, J.E., KAUFFMAN, R.G. and CASSENS, R.G. 1981. Biological detection of heterozygosity for double muscling in cattle. I. Terminal innervation ratio. J. Anim. Sci. 52: 1430-1436.

OLIVER, W.M. and CARTWRIGHT, T.C. 1968. Double muscling in cattle. A review of expression, genetics, and economic implication. Tech. Rep. No. 12, Dep. of Anim. Sci., Texas A&M University, College Station, Tex.

NOTT, C.F.G. and ROLLINS, W.C. 1979. Effects of the *m* gene for muscular hypertrophy on birth weight and growth to one year of age in beef cattle. Growth 43: 221-234.

ROLLINS, W.C., TANAKA, M., NOTT, C.F.G. and THIESSEN, R.B. 1972. On the mode of Inheritance of double-muscled conformation in bovines. Hilga. 41: 433-455.

ROLLINS, W.C., THIESSEN, F.D.C. and TANAKA, M. 1980. Effect of heterozygosity at the double-muscle locus on the performance of market calves. Hilga. 48: 1-26.

SWATLAND, H.J. 1973. Innervation of genetically enlarged muscles from double-muscled cattle. J. Anim. Sci. 36: 355-362.

SWATLAND, H.J. and CASSENS, R.G. 1974. The role of innervation in muscle development and function. J. Anim. Sci. 38: 1092-1102.

SWATLAND, H.J. and KIEFFER, N.M. 1974. Fetal development of the double muscled condition in cattle. J. Anim. Sci. 38: 752-757.

VANDEPLASSCHE, M. 1974. Die vererbung des merkmals "doppellender" und dessen bedeutung fur die rindfleischproduktion. Tierzuechter 26: 335-338.

VISSAC, B., PERREAU, B., MAULEON, P. and MENISSIER, F. 1974. Etude du caractere culard. IX--Fertilite des femelles et aptitude maternelle. Ann. Genet. Sel. anim. 6: 35-48.

WEST, R.L. 1974. Red to white fiber ratio as an index of double muscling in beef cattle. J. Anim. Sci. 38: 1165-1175.

II. EFFECT OF MILD STRESSORS ON DOUBLE MUSCLED CATTLE

A. Abstract

The effects of mild stressors were studied on three double muscled (DM) bulls and three of their phenotypically normal-to-moderate muscled (carrier) half-siblings of the same age and sex. At 14 mo of age the effect of a 4 d fast was studied. In both animal types plasma free fatty acid (FFA) concentrations more than doubled ($p<0.01$) during fasting. Plasma FFA concentrations in the DM animals were lower than those in carrier animals in both the fed and fasted states ($p<0.05$). During the fast blood urea nitrogen (BUN) concentration decreased in the carrier cattle from 10.0 mg/dL to 5.7 mg/dL and increased in the DM cattle from 9.3 mg/dL to 12.2 mg/dL ($p<0.05$). There were no significant effects on blood lactic and pyruvic acids or on plasma glucose and electrolyte concentrations. Serum cortisol concentration was elevated ($p<0.05$) from 6.3 ng/mL to 9.2 ng/mL in the fasted state in both animal types. During the fast, triiodothyronine (T_3) concentration decreased from 3.1 to 0.7 ng/dL in the DM cattle and remained unchanged (2.6 to 2.4 ng/dL) in the carrier cattle. The 3 h metabolic rate of both animal types decreased in the fasted state ($p<0.05$). The higher BUN concentration and the lower FFA concentration during fasting in the DM cattle suggests that this animal type relied to a greater extent on its protein reserves for energy substrates.

At 18 mo of age the effect of a 3 d heat exposure was studied on the same animals. Blood samples were collected and physiological parameters were monitored at 10°C and after 3 d at 26°C. The mean rectal temperature of the carriers remained constant at 38.5°C, while that of the DM bulls was elevated from 38.6°C to 39.6°C ($p<0.05$). The respiratory frequency was elevated ($p<0.01$) for both animal types at 26°C and this increased frequency was higher ($p<0.05$) for the DM bulls than for the carrier bulls. At 26°C, serum T_3 concentration decreased from 2.1 to 1.3 ng/mL for the DM bulls, while no change (1.5 to 1.6 ng/mL) occurred for the carrier bulls ($p<0.01$). Reverse-triiodothyronine concentration was lower ($p<0.05$) in the DM animals as compared with carrier animals. There were no significant effects on plasma glucose, BUN, blood lactic acid, serum thyroxine and cortisol, or plasma adrenaline and noradrenaline concentrations. The elevated rectal temperature of DM cattle during the heat stress may have been a result of an impairment in a heat loss mechanism.

B. Introduction

The double muscled (DM) syndrome is a genetic condition in beef cattle which is characterized by a generalized skeletal muscle hypertrophy (Ansay and Hanset 1979). The DM syndrome is inherited by a single pair of recessive genes which can be modified by genetic and environmental factors (Rollins et al. 1972). Affected animals have enlarged

forelimb, thigh and neck muscles (Oliver and Cartwright 1968). The prominence of the enlarged muscles of DM cattle are visually enhanced by the animal's thinner hide and reduced amounts of subcutaneous fat (Oliver and Cartwright 1968). Hanset et al. (1979) have observed that the feed consumption by DM bulls was less than normal bulls and that the DM bulls had a superior feed conversion efficiency. Considering the above characteristics, DM cattle would appear to be relatively superior beef animals.

There are some serious disadvantages associated with cattle displaying the DM syndrome which limit their apparent value to livestock production. Vissac et al. (1974) have reported that puberty is delayed, abnormal estrous cycles may occur and calving difficulties, still-borns and caesarian sections are relatively common in DM cows. Cattle displaying the DM syndrome are more susceptible to various stressors. Holmes et al. (1972b) have suggested that they are more temperamental during stress, possibly because of the development of lactic acidosis. After a severe exercise stress, a DM heifer collapsed and developed myoglobulinuria due to lactic acidosis (Holmes et al. 1972a). Monin and Boccard (1974) observed that DM animals often develop metabolic acidosis during exercise, and partially attributed the condition to the proportionally smaller heart and lungs and the lower hematocrit of this cattle type. Similarly, Holmes et al. (1973) observed that the combination of bleeding and fasting was more stressful for DM cattle

compared to normal cattle as indicated by blood metabolites and by high post-slaughter muscle pH measurements.

The University of Alberta maintains a small herd of DM cattle, and several of the most muscular animals in this herd have died suddenly; post mortem examinations have no specific cause of death. Most of the previous studies concerning effects of stress on the physiology of DM cattle have involved relatively severe stressors. The objective of the experiments reported herein was to determine the response of DM bulls to relatively mild stressors and to compare this response to that obtained with phenotypically normal bulls from a similar genetic background.

C. Materials and Methods

All animals used in the following two studies were from the double muscled herd maintained at The University of Alberta's Beef Research Ranch. Cattle within the DM breed group were phenotypically categorized (Basarab 1981) as either extreme in muscling (DM) or normal-to-moderate in muscling (carrier).

Study I

The effect of a 4 d fast was studied on three carrier, 14 mo old bulls, and three of their DM half-siblings. The animals were housed together and group fed twice-daily (0730 and 1600 h) 13 kg of a concentrate ration and grass hay was provided ad libitum. Water and mineralized salt were available free choice. During the experimental period food

was withheld for 4 d, while water and mineralized salt were available ad libitum.

The cattle were kept in metabolic crates during the experiment and had indwelling jugular vein catheters inserted the day before the experimental period. Blood samples were collected at 1000, 1100 and 1200 h in both the fed state and after the 4 d fast. Blood lactic acid (Sigma No. 826-UV, St. Louis, MO) and pyruvic acid (Sigma No. 726-UV, St. Louis, MO) concentrations were determined in whole blood and plasma glucose concentration was estimated by an enzymatic procedure (Sigma No. 115-A, St. Louis, MO). Plasma creatinine, blood urea nitrogen (BUN) and plasma electrolytes were determined by a Technicon SMA-7 (Tarrytown, NY).

Long chain free fatty acids (FFA) concentrations in the plasma were assayed by the colourimetric method described by Smith (1975). Thyroxine (T_4) and triiodothyronine (T_3) were measured in serum by standard radioimmunoassays (Diagnostic Products Corp., Los Angles, CA) and serum cortisol concentration was measured by a commerical radioimmunoassay kit (Micromedic System, Horsham, PA). Metabolic rate was estimated by indirect calorimetry based on respiratory gas patterns for a 3 h period in both the fed and fasted states (Young et al. 1975).

The statistical analysis of the data was by analysis of variance (Steel and Torrie 1980). Preliminary observation of the statistical analysis indicated that the appropriate

error mean squares for a parameter did not differ between treatments, so a pooled standard error of the mean was calculated.

Study II

The same animals were used at 18 mo of age to study the effect of a 3 d heat stress. Prior to this study, the animals were housed outdoors and the mean temperature during a two-week period prior to the study was approximately -10°C. The animals were fed a grass hay diet ad libitum and had free access to mineralized salt and water prior to, and during the experimental period.

The animals had indwelling jugular vein catheters inserted before the experimental period and were housed indoors at 10°C for 1 d, after which the room temperature was raised and maintained at 26°C for 3 d. Blood samples were collected and physiological parameters were measured at 1000, 1200 and 1400 h at 10°C and after 3 d at 26°C. The concentrations of plasma glucose, plasma creatinine, BUN, T_4, T_3, cortisol and blood lactic acid were measured as in the fasting study. Plasma bicarbonate was estimated by a Technicon SMA-7 (Tarrytown, NY) and reverse-triiodothyronine (rT_3) concentration was determined by a commercial radioimmunoassay kit (Serono Laboratories, Inc., Braintree, MA). Plasma adrenaline and noradrenaline concentrations were estimated by a radioenzymatic assay (Peuler and Johnson 1977) employing modifications described by Graham et al. (1981).

Respiratory rate was measured visually, heart rate by ECG needle electrodes inserted into the hide of each animal and an ECG recorder (Hewlett-Packard, Mississauga, Ont.). Rectal temperature was measured using a thermistor probe and telethermometer (Yellow Springs Instrument Co., Inc., Yellow Springs, OH) Statistical analysis of the data was by analysis of variance (Steel and Torrie 1980). Preliminary observation of the statistical analysis indicated that the appropriate error mean squares for a parameter did not differ between treatments, so a pooled standard error of the mean was calculated.

D. Results

Study I

The results for the effects of the fasting stress are presented in Table II.1. There were no significant differences in blood lactic and pyruvic acid or in plasma glucose and electrolyte concentrations between phenotype or treatment. Plasma creatinine concentration tended to be elevated ($p<0.1$) during the fast in both animal types. The DM animals had a higher ($p<0.05$) plasma creatinine concentration in both the fed and fasted states. In both animal types, plasma FFA concentrations more than doubled ($p<0.01$) after a 4 d fast. Plasma FFA concentrations in DM animals were consistantly lower than in carrier animals ($p<0.05$). A significant ($p<0.05$) phenotype by stressor interaction was observed for BUN concentration. Blood urea

nitrogen concentrations were similar in the two animal types during feeding, but during the fast the level decreased in the carrier cattle from 10.0 mg/dL to 5.7 mg/dL and increased in the DM cattle from 9.3 mg/dL to 12.2 mg/dL (Table II.2).

Serum cortisol concentration was significantly elevated ($p<0.05$) in the fasted state to 9.2 ng/mL as compared to the fed state value of 6.3 ng/mL in both animal types. No difference was observed for serum T_4 concentration between the animal types or to the effect of the fast. A significant ($p<0.05$) phenotype by treatment interaction was observed for T_3 concentration. During the fast the serum T_3 concentration decreased from 3.1 to 0.7 ng/dL in the DM cattle but remained unchanged (2.6 to 2.4 ng/dL) for the carrier cattle (Table II.2). The 3 h metabolic rate of both animal types decreased ($p<0.05$) from an average of 24.4 $kJ/kg^{0.75}/h$ in the fed state to 17.6 $kJ/kg^{0.75}/h$ in the fasted state.

Study II

After 3 d at 26°C, the mean rectal temperature of the carriers remained constant at 38.5°C, while the mean rectal temperature of the DM bulls was significantly ($p<0.01$) elevated from 38.6°C to 39.6°C (Table II.4). There were no observable differences in heart rate between the animal types at either room temperature (Table II.3). The respiratory frequency was significantly ($p<0.01$) elevated for both animal types at the higher room temperature and this increased frequency was greater ($p<0.05$) for the DM

bulls than for the carrier bulls.

Average plasma creatinine concentration tended ($p<0.1$) to increase from 1.8 mg/dL at 10°C to 2.0 mg/dL at 26°C with DM animals having a higher ($p<0.05$) concentration at both temperatures. There was a trend ($p<0.1$) for plasma bicarbonate concentration to be less at 26°C (22.3 mEq/L) compared to 10°C (24.0 mEq/L). There were no significant effects of phenotype or stress on plasma glucose, BUN or blood lactic acid concentrations.

A significant ($p<0.01$) phenotype by temperature interaction was observed for serum T_3 concentration. At 26°C the T_3 concentration decreased from 2.1 to 1.3 ng/dL for the DM bulls, while no change (1.5 to 1.6 ng/dL) occurred for the carrier bulls (Table II.4). There was no significant effect on serum T_4 concentration, while r-T_3 concentration was lower ($p<0.05$) in DM animals at both 10° and 26°C. There were no significant effects of phenotype or the stressor on serum cortisol, plasma adrenaline nor noradrenaline concentrations.

E. Discussion

The 3 h metabolic rate of both animal types responded similarly to the fast, but the proportion of body tissues that were utilized as energy substrates may have differed. The decrease in BUN concentration during fasting for the carrier bulls and the elevated concentration for the DM bulls suggests that the DM animals relied to a relatively

greater extent on their protein reserves for energy substrates. A smaller increase in plasma FFA concentration during the fast in the DM animals supports this suggestion. The DM cattle at The University of Alberta's Ranch have been observed to be very susceptible to losing body "condition" over severe winters, suggesting that they utilize their enlarged muscles as a source of energy substrates. Holmes and Robinson (1970) have suggested that DM cattle do not mobilize fat as readily as normal cattle during periods of reduced energy intake as they observed that the plasma FFA concentrations were lower in DM cattle than in similarly treated normal muscled cattle. These workers also observed that the DM animals lost considerable muscling when fed a diet which did not meet their maintenance energy requirement but no apparent reduction in muscle mass was noted for the normal animals fed a similar diet for a 3 week period.

Holmes et al. (1973) subjected DM cattle to a 48 h fast and observed that plasma glucose concentration was higher in the DM animals compared with normal animals, and that the concentration increased with the length of the fast in both animal types. The different effect observed during fasting on plasma glucose concentration between the results of Holmes et al. (1973) and that of the present study may be due to the method of blood sampling. Holmes et al. (1973) collected blood via venipuncture, while the samples in the present study were obtained via an indwelling catheter. The effect of blood collection and fasting in the study by

Holmes et al. (1973) resulted in dark cutting meat in the carcasses of the DM animals, but no effect was observed for normal animals which were bled and fasted nor to DM animals which were only fasted (Holmes et al. 1973). Earlier, Holmes et al. (1972b) suggested that DM cattle are more excitable than normal cattle, so the frequent handling during serial blood collection may have been the cause for differences in blood glucose concentration. The non-significant effect of fasting on plasma glucose concentration in the present study, is in agreement with the results reported by Galyean et al. (1981) for beef steers fasted for approximately 4 d. Determination of the kinetics of plasma glucose in these two animal types may represent a more meaningful measure of glucose metabolism as compared with plasma glucose concentration (see Chapter III).

Halipre (1973) observed that DM cattle were more susceptible to an acute heat stress than carrier cattle. At 25°C, he determined that the rectal temperature was significantly higher for the DM animals and that the temperature difference between the animal types increased as ambient temperature increased (Halipre 1973). The heart rate and respiratory frequency were also observed to be higher in the heat stressed DM animals and he concluded that DM cattle are less tolerant to a severe heat stress than are normal cattle. The elevated rectal temperature and the higher respiratory rate observed in the present study for the DM bulls at 26°C suggests that these animals were more stressed

than the carrier bulls. The elevated rectal temperature of the DM cattle during the heat stress indicates that the heat production was temporarily greater than the rate of heat loss from these animals.

The trend for a higher plasma creatinine concentration in both animal types during the higher room temperature agrees with the results of Colditz and Kellaway (1972) who observed an increased urinary creatinine excretion in dairy heifers during heat exposure. Higher plasma creatinine concentrations in both the fasting and heat exposure studies in DM cattle is a characteristic of these animals which has been reported by Ansay and Hanset (1979). The muscular hypertrophy of the young DM bulls could only partially account for the elevated plasma creatinine concentration in these animals (Ansay and Hanset 1979) and may also reflect the suggested generalized cell membrane defect (Basarab et al. 1980).

Depressed serum T_3 concentrations for the DM bulls at 26°C suggests that a decrease in their metabolism may have been occurring which would have ultimately helped to alleviate the heat stress. Fasting the DM cattle also resulted in a depression in serum T_3 concentration. The depressed T_3 concentration in DM cattle during mild stress may also reflect a greater rate of T_3 utilization. Webster (1976) has suggested that secretion of the thyroid hormones is depressed during prolonged exposure to thermal stress. The observation that serum T_3 concentration was unchanged

for the carrier bulls suggests that these animals were not as stressed as the DM bulls at the higher room temperature.

Double muscled cattle have enlarged muscles which have an increased proportion of white muscle fibers (Ashmore and Robinson 1969). The increased capacity of the white muscle fibers for glycolytic metabolism and lactic acid production has been correlated to the more excitable temperament of DM cattle (Holmes et al. 1972b). Monin and Boccard (1974) subjected DM cattle to an exercise stress and observed the development of metabolic acidosis as a result of excess lactic acid. In addition, the recovery to pre-exercise acid-base status takes longer in DM cattle (Holmes et al. 1973). The development of relatively high concentrations of circulating lactic acid in DM cattle likely results from an increased production due to a greater proportion of white muscle fibers (Ashmore 1974) and a decreased rate of utilization due to the smaller heart and liver of this cattle type (Ansay and Hanset 1979). An excess lactic acid production appears to occur during exercise (Monin and Boccard 1974), but does not necessarily occur in DM cattle during the action of other stressors. In the present studies, lactic acid concentration was not elevated, as a result of either the fast or heat stressors. Similarly, it was not elevated by the 48 h fasting experiment of Holmes et al. (1973). Halipre (1973) observed that lactic acid concentration was elevated to similar levels for both normal and DM bulls after exposure to a severe acute heat stress.

In summary, DM cattle even respond differently than carrier cattle to mild stressors such as a fast and heat exposure as indicated by some of the more pronounced metabolic and physiological responses shown here. Differences such as lower plasma FFA and elevated BUN concentrations that occur during fasting reflect the leaner, more muscular composition of DM cattle. Double muscled cattle are very susceptible to losing body condition during underfeeding, for they utilize their enlarged muscles to a greater extent as an energy substrate. A marked depression in T_3 concentration appears to be a characteristic response of this cattle type to both fasting and a heat exposure. Double muscled cattle are more susceptible to a heat stressor, due to a possible defect in a heat loss mechanism. Heat production was temporarily greater than heat loss in DM cattle when heat stressed so that an increase in body temperature was observed. Lactic acidosis generally does not occur in DM cattle during a fast or heat stress, but may occur during an exercise stress.

F. References

ANSAY, M. and HANSET. R. 1979. Anatomical, physiological and biochemical differences between conventional and double-muscled cattle in the Belgian Blue and White breed. Livest. Prod. Sci. 6: 5-13.

ASHMORE, C.R. 1974. Phenotypic expression of muscle fiber types and some implications to meat quality. J. Anim. Sci. 38: 1158-1164.

ASHMORE, C.R. and ROBINSON, D.W. 1969. Hereditary muscular hypertrophy in the bovine: I. Histological and biochemical characterization. Proc. Soc. Exp. Biol. Med. 132: 548-554.

BASARAB, J.A. 1981. Genetic and physiological characterization of the double muscled syndrome in cattle. PhD Thesis, The University of Alberta.

BASARAB, J.A., BERG, R.T. and THOMPSON, J.R. 1980. Erythrocyte fragility in "double-muscled" cattle. Can. J. Anim. Sci. 60: 869-876.

COLDITZ, P.J. and KELLAWAY, R.C. 1972. The effect of diet and heat stress on feed intake, growth and nitrogen metabolism in Friesian, and F, Brahman x Friesian, and Brahman heifers. Aust. J. agric. Res. 23: 717-725.

GALYEAN, M.L., LEE, R.W. and HUBBERT, M.E. 1981. Influence of fasting and transit on ruminal and blood metabolites in beef steers. J. Anim. Sci. 53: 7-18.

GRAHAM, A.D., CHRISTOPHERSON, R.J. and THOMPSON, J.R. 1981. Endocrine and metabolic changes in sheep associated with acclimation to constant or intermittent cold exposure. Can. J. Anim. Sci. 61: 81-90.

HALIPRE. A. 1973. Etude du caractere culard. X--Sensibilite des bovins culards au stress thermique. Ann. Genet. Sel. anim. 5: 441-449.

HANSET, R., STASSE, A. and MICHAUX, C. 1979. Feed intake and feed efficiency in double-muscled and conventional cattle. Z. Tierzuchtg. Zuchtgsbiol. 96: 260-269.

HOLMES, J.H.G., ASHMORE, C.R. and ROBINSON, D.W. 1973. Effects of stress on cattle with hereditary muscular hypertrophy. J. Anim. Sci. 36: 684-694.

HOLMES, J.H.G., ASHMORE, C.R., ROBINSON, D.W., FINN, J.P.and O'DELL, J. 1972a. A condition resembling "Azoturia" in a "Double Muscled" heifer. Vet. Rec. 90: 625-630.

HOLMES, J.H.G. and ROBINSON, D.W. 1970. Hereditary muscular hypertrophy in the bovine: metabolic response to nutritional stress. J. Anim. Sci. 31: 776-780.

HOLMES, J.H.G., ROBINSON, D.W. and ASHMORE, C.R. 1972b. Blood lactic acid and behaviour in cattle with hereditary muscular hypertrophy. J. Anim. Sci 35: 1011-1013.

MONIN, G. and BOCCARD, R. 1974. Caracteristiques physiologiques respiratoires des bovins culards. Ann. Genet. Sel. anim. 6: 187-193

OLIVER, W.M. and CARTWRIGHT, T.C. 1968. Double muscling in cattle. A review of expression, genetics, and economic implication. Tech. Rep. No. 12, Dep. of Anim. Sci., Texas A&M University, College Station, Tex.

PEULER, J.D. and JOHNSON, G.A. 1977. Simultaneous single isotope radioenzymatic assay of plasma noreprinephrine, epinephrine and dopamine. Life Sci. 21: 625-636.

ROLLINS, W.C., TANAKA, M., NOTT, C.F.G. and THIESSEN, R.B. 1972. On the mode of Inheritance of double-muscled conformation in bovines. Hilga. 41: 433-455.

SMITH, S.W. 1975. A new salting-out technique for colorimetric free fatty acid assays. Anal. Biochem. 67: 531-539.

STEEL, R.G.D. and TORRIE, J.H. 1980. *Principles and Procedures of Statistics*. McGraw-Hill Book Co. Inc., New

York, N.Y.

VISSAC, B., PERREAU, B., MAULEON, P. and MENISSIER, F. 1974. Etude du caractere culard. IX--Fertilite des femelles et aptitude maternelle. Ann. Genet. Sel. anim. 6: 35-48.

WEBSTER, A.J.F. 1976. The influence of the climate environment on metabolism in cattle. In: *Principles of Cattle Production*. Edited by H. Swan and W.H. Broster. Butterworths, London, Boston. pp 103-120.

YOUNG, B.A., KERRIGAN, B. and CHRISTOPHERSON, R.J. 1975. A versatile respiratory pattern analyzer for studies of energy metabolism of livestock. Can. J. Anim. Sci. 55: 17-22.

Table II.1 Response of carrier and double muscled (DM) bulls to a four day fast.

	TREATMENT		PHENOTYPE[1]		
	FED	FAST	CARRIER	DM	SEM[2]
Plasma glucose (mg/dL)	75.0	69.7	72.9	71.8	4.2
Plasma FFA (uEq/L)	262	577 **	495	344 *	46
Blood lactic acid (mg/dL)	9.8	9.8	8.7	9.9	0.9
Blood pyruvic acid (mg/dL)	0.60	0.55	0.59	0.56	0.05
Plasma creatinine (mg/dL)	1.7	1.8 *	1.6	1.8	0.07
BUN (mg/dL)	9.7	9.0	7.9	10.8 *	0.5
Plasma sodium (mEq/L)	139	140	140	139	2.5
Plasma potassium (mEq/L)	4.0	4.1	4.1	4.0	0.10
Plasma chloride (mEq/L)	103	102	102	103	1.3
Thyroxine (ug/dL)	5.4	4.8	5.4	4.8	0.3
Triiodothyronine (ng/mL)	2.8	1.6 *	2.5	1.9	0.3
Cortisol (ng/mL)	6.3	9.2 *	8.2	7.4	0.6
Metabolic rate (kJ/kg$^{0.75}$/h)	24.4	17.6 *	21.4	20.6	1.6

[1] Based on a subjective score for muscling.
[2] Overall standard error of the mean.
* Asterisk in each row within each major heading indicates a significant treatment or phenotype difference ($p<0.05$).
** Asterisks in each row within each major heading indicates a significant treatment or phenotype difference ($p<0.01$).

Table II.2 Phenotype[1] by treatment interaction means[2] for carrier and double muscled bulls (DM) bulls subjected to a four day fast.

	FED		FASTED		
	CARRIER	DM	CARRIER	DM	SEM[3]
Plasma glucose (mg/dL)	74.7	75.3	71.0	68.3	6.5
Plasma FFA (uEq/L)	317	206	673	481	48
Blood lactic acid (mg/dL)	9.4	10.1	8.0	9.7	1.3
Blood pyruvic acid (mg/dL)	0.56	0.63	0.61	0.49	0.06
Plasma creatinine (mg/dL)	1.6	1.8	1.7	1.9	0.05
BUN (mg/dL)	10.0	9.3	5.7	12.3	0.8 **
Plasma sodium (mEq/L)	141	136	138	142	3.8
Plasma potassium (mEq/L)	4.0	4.0	3.9	4.1	0.1
Plasma chloride (mEq/L)	105	101	100	104	1.7
Thyroxine (ug/dL)	5.5	5.4	5.3	4.3	0.2
Triiodothyronine (ng/mL)	2.6	3.1	2.4	0.7	0.4 *
Cortisol (ng/mL)	6.6	6.1	9.8	8.6	0.1
Metabolic rate (kJ/kg$^{0.75}$/h	25.2	23.5	17.6	17.7	1.2

[1] Based on a subjective score for muscling.
[2] Three observations per mean.
[3] Standard error of the mean.
* Asterisk in a row indicates a significant phenotype by treatment difference ($p<0.05$).
** Asterisks in a row indicates a significant phenotype by treatment difference ($p<0.01$).

Table II.3 Response of carrier and double muscled (DM) bulls to a three day heat stress.

	TEMPERATURE		PHENOTYPE[1]		
	10°C	26°C	CARRIER	DM	SEM[2]
Rectal Temperature (°C)	38.6	39.0 *	38.5	39.1 *	0.1
Heart Rate (bpm)	67	71	71	67	3
Respiratory rate (rpm)	32	94 **	54	72	4
Plasma glucose (mg/dL)	72.1	70.9	73.4	69.7	2.5
Plasma creatinine (mg/dL)	1.8	2.0	1.7	2.1 *	0.1
BUN (mg/dL)	10.8	11.3	10.7	11.5	1.2
Plasma bicarbonate (mEq/L)	25.0	22.3	24.8	22.5	1.1
Blood lactic acid (mg/dL)	6.7	6.2	6.7	6.3	0.4
Thyroxine (ug/dL)	8.3	7.0	6.7	8.6	0.7
Triiodothyronine (ng/mL)	1.8	1.5	1.6	1.7	0.1
Reverse-triiodothyronine (pg/mL)	152	144	164	133 *	8
Cortisol (ng/mL)	4.7	5.7	4.3	6.1	0.8
Adrenaline (pg/mL)	171	175	152	193	16
Noradrenaline (pg/mL)	468	535	455	549	53

[1] Based on a subjective score of muscling.
[2] Overall standard error of the mean.
* Asterisk in each row within each major heading indicates a significant temperature or phenotype difference ($p<0.05$).
** Asterisks in each row within each major heading indicates a significant temperature or phenotype difference ($p<0.01$).

Table II.4 Phenotype[1] by treatment interaction means[2] for carrier and double muscled bulls (DM) bulls subjected to a three day heat stress.

	10°C		26°C		
	CARRIER	DM	CARRIER	DM	SEM[3]
Rectal Temperature (°C)	38.5	38.6	38.5	39.6	0.46**
Heart Rate (bpm)	70	65	72	69	3
Respiratory rate (rpm)	31	32	78	111	6 *
Plasma glucose (mg/dL)	73.0	71.3	73.7	68.0	3.2
Plasma creatinine (mg/dL)	1.6	2.0	1.8	2.3	0.1
BUN (mg/dL)	11.0	10.7	10.3	12.3	1.1
Plasma bicarbonate (mEq/L)	25.7	24.3	24.0	20.7	1.0
Blood lactic acid (mg/dL)	6.6	6.9	6.8	5.7	0.4
Thyroxine (ug/dL)	7.6	8.9	8.2	5.8	0.7
Triiodothyronine (ng/mL)	1.5	2.1	1.6	1.3	0.1 *
Reverse-triiodothyronine (pg/mL)	162	142	165	124	6.3
Cortisol (ng/mL)	4.2	5.2	4.4	7.0	0.6
Adrenaline (pg/mL)	152	189	162	197	16
Noradrenaline (pg/mL)	443	493	466	604	76

[1] Based on a subjective score for muscling.
[2] Three observations per mean.
[3] Standard error of the mean.
* Asterisk in a row indicates a significant phenotype by treatment difference ($p<0.05$).
** Asterisks in a row indicates a significant phenotype by treatment difference ($p<0.01$).

III. EFFECT OF FASTING ON PLASMA GLUCOSE KINETICS IN DOUBLE MUSCLED CATTLE

A. Abstract

The effect of a 4 d fast on plasma glucose kinetics was determined in three 14 mo of age normal-to-moderate (carrier) bulls and three of their double muscled (DM) half-siblings of the same sex and age. The bulls were group fed twice-daily 13 kg of a concentration ration and grass hay ad libitum. A single injection of approximately 500 uCi of 6-^{3}H-glucose was administered by means of a jugular vein catheter at 1200 h for each bull in both the fed state and after the 4 d fast. The lines of best fit for plasma glucose specific activity curves were determined by a non-linear least squares computer program.

There were no statistically significant effects of animal type or treatment on plasma glucose or blood lactic acid concentrations. The glucose entry rate during the fed state was 30.2 mg/kg$^{0.75}$/min which was significantly ($p<0.05$) greater than 18.1 mg/kg$^{0.75}$/min estimated after the 4 d fast. The irreversible loss of 7.6 mg/kg$^{0.75}$/min in the fed state was greater ($p<0.05$) than 4.1 mg/kg$^{0.75}$/min estimated after the 4 d fast. There was a trend ($p<0.1$) for the glucose pool size to be less in the fasted state for both animal types. The glucose pool size was significantly greater ($p<0.05$) in the carrier than in DM bulls (44.3 g vs 22.2 g). The lower glucose pool size in the DM bulls during both the fed and

fasted states probably reflects the relatively smaller liver and cardiovascular system in this cattle type.

B. Introduction

Cattle displaying the double muscled (DM) syndrome are characterized by relatively finer bones, reduced body fat content and enlarged skeletal muscles compared with normal cattle. (Oliver and Cartwright 1968). Hendricks et al. (1973) have suggested that the generalized muscular hypertrophy of DM cattle can be accounted for by an increased proportion and size of the white muscle fibers, while the number of the red muscle fibers is not affected. These differences in the proportion and size of skeletal muscle fibers have also been reported to be present in the DM fetus (Ashmore et al. 1974; Swatland and Kieffer 1974). Mascarello and Geroldi (1974) have studied skeletal muscle fiber types in the Piedmont breed of cattle and confirmed that the extremely heavily muscled animals commonly found in this breed also have proportionally more white muscle fibers than normal muscled animals of the breed.

Biochemically the white muscle fibers have a relatively high capacity for anaerobic metabolism as they have few mitochondria, are enzymatically adapted for glycogenolytic and glycolytic metabolism and possess relatively large glycogen reserves (Ashmore 1974). Double muscled cattle have been reported to develop a lactic acidosis when subjected to various severe stressors (Holmes et al. 1973; Monin and

Boccard 1974). These high concentrations of lactic acid in the circulatory system of DM animals may arise from an increased rate of production, a decreased rate of utilization of lactic acid or possibly a combination of both. The relatively large size of the skeletal musculature in DM cattle may account for lactic acid production exceeding its utilization. At the same time lactic acid utilization may be reduced as Ansay and Hanset (1979) have reported that the lungs and hearts of DM cattle are proportionately smaller when compared with similar sized normal muscled animals. These organs are primarily responsible for maintaining oxidative metabolism and under the influence a stressor, DM cattle may have to rely to a greater extend on anaerobic metabolism as compared to normal cattle (Holmes et al. 1972b). The liver in the DM animal has also been shown to be relatively small (Ansay and Hanset 1979) and since it is the key gluconeogenic organ in the body (Bergman 1973) lactic acid and hence glucose metabolism may be altered. The objective of this study was to determine if glucose metabolism differs between DM and phenotypically normal cattle under resting conditions and when the animals are subjected to a mild stressor.

C. Materials and Methods

The animals used in this study were from the double muscled herd maintained at The University of Alberta's Beef Research Ranch. Cattle within the DM breed group were

phenotypically categorized (Basarab 1981) as either extreme in muscling (DM) or normal-to-moderate in muscling (carrier).

The effect of a 4 d fast on plasma glucose kinetics was studied on three carrier 14-mo old bulls and three of their DM half-siblings of the same sex and age. The mean body weight after the fasting period was 432 kg for the carrier and 399 kg for the DM bulls. The animals were housed together and group fed a diet consisting of 13 kg of a concentrate ration twice-daily (0730 and 1600 h) and grass hay ad libitum. Water and mineralized salt were available free choice. During the fasting period, food was withheld for 4 d, and water and mineralized salt were available ad libitum.

The cattle were kept in metabolic crates and an indwelling catheter was placed in each jugular vein the day before the experimental period. Approximately 500 uCi of 6-^{3}H-D-glucose (New England Nuclear, Boston, MA) was injected via one of the jugular vein catheters at 1200 h in both the fed state and on the fourth day of the fast. Serial blood samples (10 mL) were collected throughout each 240 min post-injection period from the second jugular vein catheter and transferred to chilled heparinized tubes. The blood was centrifuged immediately at room temperature and the plasma was removed and stored at -20°C until analyzed.

Plasma glucose concentration was determined by an enzymatic procedure (Sigma, No. 726UV, St. Louis, MO).

Plasma glucose was separated from lactic acid by the anion-exchange procedure outlined by Schmidt et al. (1975). The eluate was collected into a scintillation vial, frozen and lyophilized in a VirTis SRC freeze-dryer (Gardiner, NY). The residue was dissolved in 1 mL distilled water and 15 mL Aquasol-2 liquid scintillation cocktail and counted in a liquid scintillation counter (Searle Mark III, Des Plaines, IL). Whole blood lactic acid concentration was measured by an enzymatic procedure (Sigma No. 826-UV, St. Louis, MO) in samples obtained at 1000, 1100 and 1200 h in both the fed state and on the fourth day of the fast.

The lines of best fit for the plasma glucose specific activity curves were determined by a BMDP (Package P3R) non-linear least squares computer program. Glucose entry rate, pool size and irreversible loss were calculated by standard procedures (e.g. Leng 1970). The data were analyzed by analysis of variance (Steel and Torrie 1980). Preliminary observation of the statistical analysis indicated that the appropiate error mean squares for a parameter did not differ between treatments, so a pooled standard error of the mean was calculated.

D. Results and Discussion

There was no significant difference observed for plasma glucose concentration between animal types or as a result of the 4 d fast (Table III.1). Holmes et al. (1973) reported that a 2 d fast resulted in a slight elevation in plasma

glucose concentration for both normal and DM animals. They also reported that the plasma glucose concentration for the DM animals was consistantly 20% higher than for the normal animals. The results of the latter study may reflect the more excitable temperament of DM animals (Holmes et al. 1972b) as the blood samples were collected via venipuncture which may have been relatively more stressful. Young et al. (1974) subjected young Holstein steers weighing an average of 186 kg to a fast and observed a decrease of approximately 24% in blood glucose concentration after 7 d. The larger size of the animals and the shorter fasting period in the present study compared with the study by Young et al. (1974) may account for differences observed in these two studies. Recently, Galyean et al. (1981) reported that the plasma glucose concentration in beef steers did not change when the animals were fasted for approximately 4 d.

An example of the time course change in plasma glucose specific activity for a DM bull during both the fed and fasted states is presented in Figure III.1. A two-component system was the best fit for the data. The mean kinetic parameters for all animals are presented in Table III.1 and Table III.2. There was no significant difference between the phenotypes for either glucose entry rate or irreversible loss. The glucose entry rate and irreversible loss were significantly ($p<0.05$) reduced in the fasted state for both animal types. The average glucose entry rate of 30.2 $mg/kg^{0.75}/min$ for the fed state is approximately 50% higher

than the value reported by Young et al. (1974) for Holstein steers. This difference may reflect the sex of the animals and the diet, as Young et al. (1974) fed a maintenance diet at intervals of 2 h, whereas the diet in the present study was above maintenance and fed twice daily. After 4 days of fasting in the present study glucose entry rate was still higher than the value obtained by Young et al. (1974) after fasting their animals for 7 days.

Glucose pool size tended ($p<0.1$) to be less in the fasted state for both animal types and was significantly ($p<0.05$) less in the DM cattle than in the carrier cattle in both the fed and fasted states. The pool size of the carrier cattle in the fed state was similar to that reported for Zebu and Zebu x Brown Swiss bulls by Ferreiro et al. (1979) but was lower than that reported by Young et al. (1974) for smaller Holstein steers. The trend for a decrease in the glucose pool size during fasting in the present study and in the study of Young et al. (1974) indicates that less glucose was in equilibrium with the sampling pool during the experimental period in the fasted state compared with the fed state. The significantly smaller glucose pool size in the DM cattle is not reflected by a lower plasma glucose concentration and may therefore result from reduced tissue glycogen stores or possibly an altered extravascular glucose tracer distribution. The smaller glucose pool size in DM cattle may be a result of smaller organs such as the liver and those of the cardiovascular system (Ansay and Hanset

1979). The smaller size and similar glycogen content (BreDahl 1969) in livers of DM cattle compared with normal cattle indicate that the total glycogen content in livers of DM cattle may be reduced, which is possibly reflected by the smaller glucose pool size. Double muscled cattle probably have a greater total amount of glycogen stored in their skeletal muscles due to the increased number of the larger white muscle fibers which contain relatively more glycogen than red muscle fibers (Ashmore 1974). Muscle cannot directly contribute glucose to the plasma pool for skeletal muscle cells have extremely low glucose-6-phosphatase activity (Surholt and Newsholme 1981). Employing the plasma volume proportion obtained by Degan and Young (1980) for sheep, it would appear that the glucose pool size for the DM bulls in the fasted state can be accounted for by the glucose located in the plasma, indicating that a different distribution of the glucose tracer may exist between the two cattle types. Interpretation of kinetic parameters in terms of anatomical boundaries should be performed with caution, as the mathematical model may not represent specific anatomical pools (Kronfeld 1977).

Double muscled cattle have been reported to be more stress susceptible as compared with normal cattle and excess stress may result in a physiological imbalance such as metabolic acidosis. Monin and Boccard (1974) and Holmes et al. (1973) have reported that lactic acidosis occurs in DM cattle during rigorous exercise which may result in severe

muscle damage as indicated by myoglobinuria (Holmes et al. 1972a). In the present study lactic acid concentration was not elevated as a result of the fast nor was it elevated by the fasting experiment of Holmes et al. (1973) indicating that fasting may not be a severe enough stressor to have a major effect on lactate metabolism.

In summary, it appears that glucose metabolism, as measured by plasma glucose kinetics, in resting fed or fasted DM animals does not differ from their normal-to-moderate muscled half-siblings. Also, both DM and carrier cattle respond in a similar manner to a fast as irreversible loss, total entry rate and glucose pool size were less in the fasted state as compared with the fed state in both animal types. The significantly smaller glucose pool size in DM bulls in both the fed and fasting states probably reflects the proportionately smaller size of both the liver and the cardiovascular system in DM cattle. Although the DM cattle used in this study do not have an apparent altered whole body glucose metabolism in the fed state and after a 4 d fast when compared to their half-sibling carriers, they may have when subjected to sudden and severe stressors such as exercise involving increased activity of their skeletal musculature as has been shown to occur in other studies.

E. References

ANSAY, M. and HANSET. R. 1979. Anatomical, physiological and biochemical differences between conventional and double-muscled cattle in the Belgian Blue and White breed. Livest. Prod. Sci. 6: 5-13.

ASHMORE, C.R. 1974. Phenotypic expression of muscle fiber types and some implications to meat quality. J. Anim. Sci. 38: 1158-1164.

ASHMORE, C.R., PARKER, W., STOKES, H. and DOERR, L. 1974. Comparative aspects of muscle fiber types in fetuses of the normal and "double-muscled" cattle. Growth 38: 501-506.

BASARAB, J.A. 1981. Genetic and physiological characterization of the double muscled syndrome in cattle. PhD Thesis, The University of Alberta.

BERGMAN, E.N. 1973. Glucose metabolism in ruminants as related to hypoglycemia and ketosis. Cornell Vet. 63: 341-382.

BREDAHL, R.L. 1969. Some physical and physiological comparisons between Double Muscled and normal cattle. MSc Thesis, Iowa State University.

DEGAN, A.A. and YOUNG, B.A. 1980. Effect of cold exposure on liveweight and body fluid compartments in sheep. Can. J. Anim. Sci. 60:33-41.

FERREIRO, H.M., PRIEGO, A., LOPEZ, J., PRESTON, T.R. and LENG, R.A. 1979. Glucose metabolism in cattle given sugar cane based diets supplemented with varying quanties of rice polishings. Br. J. Nutr. 42:341-347.

GALYEAN, M.L., LEE, R.W. and HUBBERT, M.E. 1981. Influence of fasting and transit on ruminal and blood metabolites in beef steers. J. Anim. Sci. 53: 7-18.

HENDRICKS, H.B., ABERLE, E.D., JONES, D.J. and MARTIN, T.G.

1973. Muscle fiber type, rigor development and bone strength in double muscled cattle. J. Anim. Sci. 37: 1305-1311.

HOLMES, J.H.G., ASHMORE, C.R. and ROBINSON, D.W. 1973. Effects of stress on cattle with hereditary muscular hypertrophy. J. Anim. Sci. 36: 684-694.

HOLMES, J.H.G., ASHMORE, C.R., ROBINSON, D.W., FINN, J.P. and O'DELL, J. 1972a. A condition resembling "Azoturia" in a "Double Muscled" heifer. Vet. Rec. 90: 625-630.

HOLMES, J.H.G., ROBINSON, D.W. and ASHMORE, C.R. 1972b. Blood lactic acid and behaviour in cattle with hereditary muscular hypertrophy. J. Anim. Sci. 35:1011-1013.

KRONFELD, D.S. 1977. Glucose transport and recycling determined by means of two tracers and multicompartmental analysis. Federation Proc. 36: 259-264.

LENG, R.A. 1970. Glucose synthesis in ruminants. Adv. Vet. Sci. Comp. Med. 14: 209-260.

MASCARELLO, F. and GEROLDI, R. 1974. Tipizzazione delle fiber muscolari in bovini Piedmontese "della coscia". Atti Soc. It. Sci. Vet. 27: 458-460.

MONIN, G. and BOCCARD, R. 1974. Caracteristiques physiologiques respiratoires des bovins culards. Ann. Genet. Sel. anim. 6: 187-193.

OLIVER, W.M. and CARTWRIGHT, T.C. 1968. Double muscling in cattle. A review of expression, genetics, and economic implication. Tech. Rep. No. 12, Dep. of Anim. Sci., Texas A&M University, College Station, Tex.

SCHMIDT, S.P., SMITH, J.A. and YOUNG, J.W. 1975. Rapid determination of (Carbon-14) glucose specific radioactivity for in vivo glucose kinetics. J. Dairy Sci. 58: 952-956.

STEEL, R.G.D. and TORRIE, J.H. 1980. Principles and

Procedures of Statistics. McGraw-Hill Book Co. Inc., New York, N.Y.

SURHOLT, B. and NEWSHOLME, E.A. 1981. Maximum activities and properties of glucose 6-phosphatase in muscles from vertebrates and invertebrates. Biochem. J. 198: 621-629.

SWATLAND, H.J. and KIEFFER, N.M. 1974. Fetal development of the double muscled condition in cattle. J. Anim. Sci. 38: 752-757.

YOUNG, J.W., TROTT, D.R., BERGER, P.J., SCHMIDT, S.P. and SMITH, J.A. 1974. Gluconeogenesis in ruminants: glucose kinetic parameters in calves under standardized conditions. J. Nutr. 104: 1049-1055.

Table III.1 Mean[1] glucose and lactic acid concentrations, glucose pool size, total entry rate (TER) and irreversible loss (IRL) calculated from a single injection of ^{3}H-glucose in carrier and double muscled (DM) bulls subjected to a four day fast.

	TREATMENT		PHENOTYPE[2]		
	FED	FAST	CARRIER	DM	SEM[3]
Plasma glucose (mg/dL)	77.2	67.9	73.1	72.0	4.6
Blood lactic acid (mg/dL)	9.8	8.9	8.7	9.9	0.9
Pool size (g)	37.6	28.9	44.3	22.2 *	4.7
TER ($mg/kg^{0.75}/min$)	30.2	18.1 *	23.6	24.8	2.9
IRL ($mg/kg^{0.75}/min$)	7.6	4.1 *	6.2	5.6	0.9

[1] Six observations per mean.
[2] Based on a subjective score for muscling.
[3] Overall standard error of the mean.
* Asterisk in each row within each major heading indicates a significant treatment or phenotype difference ($p<0.05$).

Table III.2 Phenotype[1] by treatment interaction means[2] for glucose and lactic acid concentrations, glucose pool size, total entry rate (TER) and irreversible loss (IRL) calculated from a single injection of ^{3}H-glucose in carrier and double muscled (DM) bulls subjected to a four day fast.

	FED		FASTED		
	CARRIER	DM	CARRIER	DM	SEM[3]
Plasma glucose (mg/dL)	79.0	75.4	67.2	68.6	6.1
Blood lactic acid (mg/dL)	9.4	10.1	8.0	9.7	1.3
Pool size (g)	47.2	27.8	41.3	14.5	5.3
TER (mg/kg$^{0.75}$/min)	26.9	33.5	20.2	16.0	4.1
IRL (mg/kg$^{0.75}$/min	7.2	8.0	5.1	3.1	1.3

[1] Based on a subjective score for muscling.
[2] Three observations per mean.
[3] Standard error of the mean.

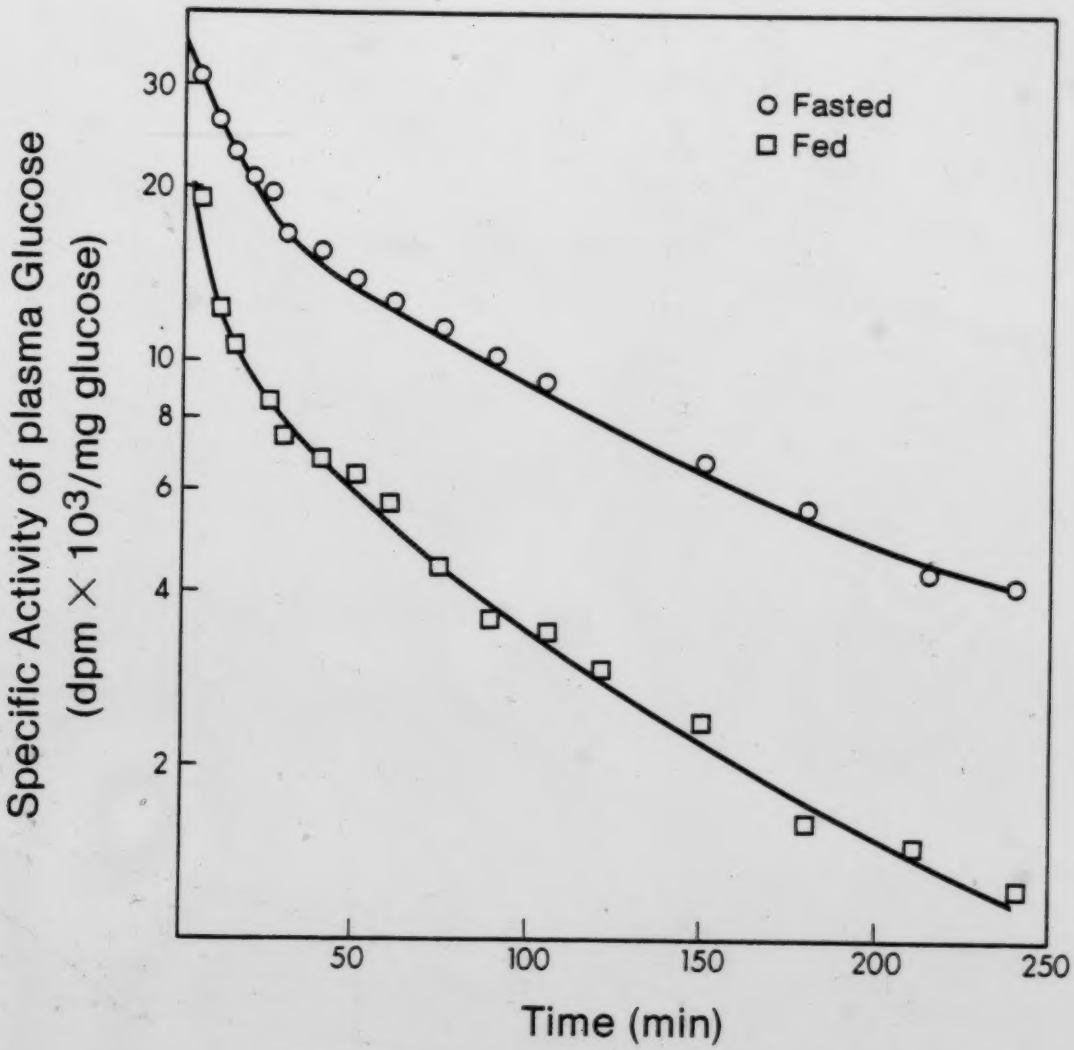

Figure III.1 An example of glucose specific activity curves for a double muscled bull in the fed state and after a four day fast following single injection of 6-^{3}H-glucose.

IV. SOME KINETIC PARAMETERS OF SERUM TRIIODOTHYRONINE AND METABOLIC RATE OF DOUBLE MUSCLED CATTLE

A. Abstract

Kinetic parameters of serum triiodothyronine (T_3) and metabolic rate (MR) were determined in double muscled (DM) and phenotypically normal-to-moderate muscled (carrier) cattle. Three carrier, 19 mo old bulls and three of their DM half-siblings were fed grass hay diet ad libitum. Approximately 1 mCi of ^{125}I-T_3 was injected into a jugular vein catheter and serial blood samples were collected from a second catheter for 12 h post-injection. The specific activity of serum T_3 was determined by a modified radioimmunoassay procedure. Kinetic parameters of serum T_3 such as pool size, irreversible loss (IRL) and total entry rate (TER) were calculated by standard methods. The T_3 pool size was higher ($p<0.001$) in DM as compared to carrier cattle which probably reflects the reported higher serum T_3 concentration of this animal type. A trend ($p<0.1$) for IRL of T_3 to be greater in DM cattle was observed, whereas TER for T_3 in the DM cattle was not observed to be significantly different from carrier cattle.

The MR for 24 h was determined for four DM and four carrier bulls. Within each animal type there were two yearlings and two 3 yr old animals, all of which were fed grass hay ad libitum up until 12 h before the experimental period. The calculated daily MR of 415 kJ/kg$^{0.75}$/d estimated

for the DM bulls was higher ($p<0.05$) than 366 kJ/kg$^{0.75}$/d for the carrier bulls. Also, the MR of 424 kJ/kg$^{0.75}$/d for the yearling bulls was higher ($p<0.05$) than 357 kJ/kg$^{0.75}$/d for the 3 yr old bulls. The larger T_3 pool size, the trend towards an increased T_3 IRL and the elevated MR of DM cattle are strongly suggestive that this animal type is relatively hyperthyroid.

B. Introduction

The double muscled (DM) syndrome in cattle is a genetic condition which is characterized by an enlargement of skeletal muscles, reduced body fat, and by relatively small internal organs in affected animals (Oliver and Cartwright 1968). The generalized muscular hypertrophy of DM cattle is a result of an increased number of the larger white muscle fibers, while the number of red muscle fibers is not affected (Hendricks et al. 1973). A faster rate of gain and an improved feed conversion efficiency up until a year of age in some DM populations, as well as the production of leaner carcasses would appear to make DM cattle a superior beef cattle type (Oliver and Cartwright 1968). Disadvantages associated with DM cattle production are the poor reproductive performance of the females (Vissac et al. 1974) and the observation that DM cattle are more stress susceptible compare to normal cattle (Holmes et al. 1973).

The etiology of stress susceptible (SS) swine has been more extensively studied than that of DM cattle. There are

numerous similarities between DM cattle and SS swine. The genetics of both of these conditions are similar and phenotypically these animal types are lean, muscular and more stress susceptible than normal animals of their species (Ashmore 1974). There is an increased proportion of the white muscle fibers in their enlarged muscles and excess pre-slaughter stress may result in poor quality carcasses (Ashmore 1974). Relatively fragile erythrocytes (Cheah and Cheah 1979) and a sensitivity to the anaesthetic halothane (Eikelenboom and Minkema 1974) have been reported in SS swine. Additional physiological characteristics of SS swine include increased serum thyroxine (T_4) concentration (Eikelenboom and Weiss 1972) and T_4 turnover (Marple 1977), and elevated basal metabolic rate (Sundstol et al. 1979). Marple et al. (1977) have reported an increased metabolic clearance rate of triiodothyronine (T_3) in SS swine and have suggested that the increased heat production in these animals may be a result of over stimulation of the sarcoplasmic reticulum by thyroid hormones. Basarab (1981) has observed that the concentration of the thyroid hormone T_3 is higher in DM cattle. The objectives of this study were to determine some kinetic parameters of serum T_3 and to estimate the metabolic rate of double muscled cattle and compare these results to phenotypically normal cattle.

C. Materials and Methods

All animals used in the following two studies were from the double muscled herd maintained at The University of Alberta'a Beef Research Ranch. Cattle within the DM breed group were phenotypically categorized (Basarab 1981) as either extreme in muscling (DM) or normal-to-moderate in muscling (carrier).

Study I

Three carrier, 19 mo old bulls and three of their DM half-siblings were housed together and were accustomed to handling. The animals were fed a grass hay diet ad libitum and had free access to mineralized salt and water prior to, and during the experimental period.

The cattle were kept in metabolic crates and an indwelling catheter was inserted into each jugular vein the day before the experimental period. Approximately 1 mCi of ^{125}I-T_3 (New England Nuclear, Boston, MA) was mixed with 10 mL of autogenous plasma and injected via one of the jugular vein catheters. Serial blood samples (10 mL) were collected from the second jugular vein catheter and allowed to clot in centrifuge tubes for 3 h. The samples were centrifuged and the serum was removed and stored at -20°C until analyzed.

The serum concentration of T_3 was determined by radioimmunoassay (Chopra et al. 1972). Radioactivity arising from the injected tracer was accounted for by incubating each serum sample in duplicate with an equal volume of buffer (sample blank) in place of the radioactive antigen.

The total tracer radioactivity located in serum T_3 was then estimated by dividing the counts in the sample blank by the percent bound T_3 and multiplying this value by 100%. The percent bound T_3 was calculated during the T_3 concentration determination for each sample. The specific activity of each sample was determined by dividing the counts associated with T_3 by the amount of T_3 in the respective serum sample. The lines of best fit for the serum T_3 specific activity values were determined by a BMDP (Package P3R) non-linear least squares computer program. Triiodothyronine total entry rate, pool size and irreversible loss were calculated by standard procedures used for other blood metabolites (e.g., Leng 1970). The means were compared statistically by use of the Student t-test (Steel and Torrie 1980).

Study II

In this study four carrier bulls and four of their DM half-siblings from the DM population were used. Within each animal type there were two yearlings and two 3 yr old animals. Prior to the experimental period, the animals were accustomed to having their heads inserted into a respiratory hood. The animals were fed a grass hay diet ad libitum and had free access to mineralized salt and water prior to the experimental period.

The cattle were placed in metabolic crates and all feed was removed at 2000 h the day before the experimental period. The 24 h metabolic rate was estimated by indirect calorimetry by the procedure of Young et al. (1975) starting

at 0800 h the morning following the removal of feed. Water was available to the animals during the metabolic rate determination. The data were statistically analyzed by analysis of variance (Steel and Torrie 1980).

D. Results and Discussion

An example of the time course change of serum T_3 specific activity is presented in Figure IV.1. The data were best represented by a two-component system and the calculated kinetic parameters are listed in Table IV.1. The T_3 pool size for the DM bulls of 1.01 mg was higher ($p<0.001$) than that of 0.49 mg estimated for the carrier bulls. Irreversible loss values for T_3 tended ($p<0.1$) to be higher for the DM animals compared to the carrier animals. Mean T_3 entry rates for the DM bulls and the carrier bulls did not differ significantly.

Direct comparison of the T_3 kinetic data reported in this study to that reported in the literature is complicated by the different methods of estimation of parameters. Irreversible loss in this study is synonymous to the term turnover rate of other workers (Leng 1970). The estimate of T_3 irreversible loss in this study agrees with the value of the turnover rate of T_3 reported by Erenberg et al. (1973) for pregnant sheep when expressed on a metabolic weight basis. The large T_3 entry rate compared with the T_3 irreversible loss probably reflects the exchange taking place between serum T_3 and other compartmental pools.

The larger T_3 pool size in the DM animals probably reflects the elevated serum T_3 concentration as reported by Basarab (1981) in DM cattle relative to carrier and normal cattle. The significantly lower serum concentration of reverse-triiodothyronine (see Chapter II) in DM cattle compared to carrier cattle supports the observation of elevated serum T_3 concentration in this cattle type as serum concentrations of reverse-triiodothyronine are normally inversely related to serum concentrations of T_3 (Bernal and Refetoff 1977). Recently, Novakofski and Kauffman (1981) reported lower serum T_3 levels in DM cattle. Differences in the reported serum T_3 concentrations may reflect the influence of stress prior to blood sampling as the effect of both fasting and heat exposure have been shown (see Chapter II) to result in a depression in serum T_3 concentration in DM bulls while the levels in carrier bulls remained relatively constant. A more meaningful measure of thyroid hormone status may be obtained by kinetic studies (Marple et al. 1977). The trend towards an increased T_3 irreversible loss in DM bulls relative to carriers indicates a higher rate of metabolism of T_3 in DM cattle. Marple et al. (1977) have reported that SS swine, which are muscular and lean like DM cattle, have a higher rate of metabolism of T_3 as well as T_4 relative to normal swine. Standal et al. (1980) have reported the rate constant for T_3 degradation and the T_3 concentrations were higher for a line of pigs selected for high rate of gain and low backfat thickness compared to

a line of pigs selected for low rate of gain and high backfat thickness.

The estimated daily metabolic rate of 415 kJ/kg$^{0.75}$/d estimated for the DM bulls was significantly higher ($p<0.05$) than 366 kJ/kg$^{0.75}$/d estimated for the normal carrier bulls (Table IV.2). Similarly, the metabolic rate (424 kJ/kg$^{0.75}$/d) for the yearling bulls was significantly higher ($p<0.05$) than that (357 kJ/kg$^{0.75}$/d) for the 3 yr old bulls (Table IV.2). These values fall in the range of estimates surveyed by Webster (1978) and are consistent with the trend for relatively higher metabolic rates in younger animals.

The metabolic rate of both SS swine and DM cattle appears to be elevated above that of normal muscled animals of the same species. Williams et al. (1977) have shown that the lean and muscular SS swine have a higher basal metabolic rate than normal swine. Sundstol et al. (1979) compared the metabolic rates of pigs selected for reduced backfat and rapid rate of gain (lean) to pigs selected for increased backfat and slow rate of gain (fat) and observed that the "lean" pigs had an elevated metabolic rate. Similarly, Pullar and Webster (1977) estimated the maintenance requirements of lean and fat Zucker rats and observed that the leaner rats produced more heat per unit body weight. Recently, experimental evidence has prompted the speculation that the maintenance requirements (Hanset et al. 1979) and the metabolic rate (Kolataj et al. 1979) of DM cattle are higher relative to normal cattle of the same weight. The

present study agrees with this speculation.

The elevated concentration of serum T_3 (Basarab 1981), the significantly larger T_3 pool size and the trend towards an increased T_3 irreversible loss in DM cattle, plus the observation that DM cattle have an elevated metabolic rate are strongly suggestive that this animal type is relatively hyperthyroid. Similar observations have been reported for both lean rats (Pullar and Webster 1977) and lean pigs (Marple et al. 1977).

E. References

ASHMORE, C.R. 1974. Phenotypic expression of muscle fiber types and some implications to meat quality. J. Anim. Sci. 38: 1158-1164.

BASARAB J.A. 1981. Genetic and physiological characterization of the double-muscled syndrome in cattle. PhD Thesis, The University of Alberta.

BERNAL, J. and REFETOFF, S. 1977. The action of thyroid hormones. Clin. Endocrinol. 6: 227-249.

CHEAH, K.S. and CHEAH, A.M. 1979. Mitochondrial calcium, erythrocyte fragility and porcine malignant hyperthermia. FEBS Letters 107: 265-268.

CHOPRA, I.J., HO, R.S. and LAM, R. 1972. An improved radioimmunoassay of triiodothyronine in serum: Its application to clinical and physiological studies J. Lab. Clin. Med. 80: 729-739.

EIKELENBOOM, G. and MINKEMA, D. 1974. Prediction of pale, soft, exudative muscle with a non-lethal test for the halothane-induced porcine malignant hyperthermia syndrome. Tijdschr. Diergeneesk. 99: 421-426.

EIKELENBOOM, G. and WEISS, G.M. 1972. Breed and exercise influence on T_4 and PSE. J. Anim. Sci. 35: 1096 (Abst.).

ERENBERG, A., OMORI, D., Oh, W. and FISHER, D.A. 1973. The effect of fetal thyroidectomy on thyroid hormone metabolism in maternal and fetal sheep. Pediat. Res. 7: 870 -877.

HANSET, R., STASSE, A. and MICHAUX, C. 1979. Feed intake and feed efficiency in double-muscled and conventional cattle. Z. Tierzuchtg. Zuchtgsbiol. 96: 260-269.

HENDRICKS, H.B., ABERLE, E.D., JONES, D.J. and MARTIN, T. Muscle fiber type, rigor development and bone strength in double muscled cattle. J. Anim. Sci. 37: 1305-1311.

HOLMES, J.H.G., ASHMORE, C.R. and ROBINSON, D.W. 1973. Effects of stress on cattle with hereditary muscular hypertrophy. J. Anim. Sci. 36: 684-694.

KOLATAJ, A., REKLEWSKI, Z., DEMBOWSKI, J., TYRAWSKA-SPYCHALOWA, D. and DZIEWIECKI, C. 1979. Physiological aspects of muscular hypertrophy in cattle. I. Activity of some enzymes in blood plasma. Z. Tierzuchtg. Zuchtgsbiol. 95: 222-226.

LENG, R.A. 1970. Glucose synthesis in ruminants. Adv. Vet. Sci. Comp. Med. 14: 209-260.

MARPLE, D.N. 1977. Physiological factors causing stress-susceptibility. Proceedings 30th Annual Reciprocal Meat Conference. Alabama. pp 170-176.

MARPLE, D.N., NACHREINER, R.F., PRITCHETT, J.F., MILLES, R.J., BROWN, H.R. and NOE, L.S. 1977. Thyroid and sarcoplasmic reticulum function in halothane-sensitive swine. J. Anim. Sci. 45: 1375-1381.

NOVAKOFSKI, J.E. and KAUFFMAN, R.G. 1981. Biological detection of heterozygosity for double muscling in cattle. II. Thyroid hormone concentrations. J. Anim. Sci. 52: 1437-1441.

OLIVER, W.M. and CARTWRIGHT, T.C. 1968. Double muscling in cattle. A review of expression, genetics, and economic implication. Tech. Rep. No. 12, Dep. of Anim. Sci., Texas A&M University, College Station, Tex.

PULLAR, J.D. and WEBSTER, A.J.F. 1977. The energy cost of fat and protein deposition in the rat. Br. J. Nutr. 37: 355-363.

STANDAL, N., BORGHILD, T., EGGUM, A. and DAHL, P.M. 1980. Thyroxine and triiodothyronine degradation in lines of pigs selected for rate of gain and thickness of backfat. Acta. Agric. Scand. 30: 201-204.

STEEL, R.G.D. and TORRIE, J.H. 1980. *Principles and Procedures of Statistics*. McGraw-Hill Book Co. Inc., New York, N.Y.

SUNDSTOL, F., STANDAL, N. and VANGEN, O. 1979. Energy metabolism in lines of pigs selected for thickness of backfat and rate of gain. Acta Agric. Scand. 29: 337-345.

VISSAC, B., PERREAU, B., MAULEON, P. and MENISSIER, F. 1974. Etude du caractere culard IX--Fertilite des femelles et aptitude maternelle. Ann. Genet. Sel. anim. 6: 35-48.

WEBSTER, A.J.F. 1978. Prediction of the energy requirements for growth in beef cattle. Wld Rev. Nutr. Diet 30: 189-226.

WILLIAMS, C.H., SHANKLIN, M.D., HEDRICK, H.B., MUHRER, M.E., STUBBS, D.H., KRAUSE, G.F., PAYNE, C.G., BENEDICT, J.D., HUTCHESON, D.P., LASLEY, J.F. and TRUMAN. H.S. 1977. The fulminant hyperthermia-stress syndrome: genetic aspects, hemodynamic and metabolic measurements in susceptible and normal pigs. In: *The Second International Symposium on Malignant Hyperthermia*. Edited by J.A. Aldrete and B.A. Britt. Grune & Stratton Publishers, New York. pp 113-146.

YOUNG, B.A., KERRIGAN, B. and CHRISTOPHERSON, R.J. 1975. A versatile respiratory pattern analyzer for studies of energy metabolism of livestock. Can. J. Anim. Sci. 55: 17-22.

Table IV.1 Mean[1] triiodothyronine (T_3) pool size, total entry rate (TER) and irreversible loss (IRL) calculated from a single injection of ^{125}I-T_3 in carrier and double muscled (DM) bulls.

Phenotype[2]	Carrier	DM	SEM[3]
Pool Size (mg)	0.49	1.01	0.09***
TER (ug/min)	9.5	12.9	2.3
IRL (ug/min)	0.48	0.82	0.20

[1] Three animals per mean.
[2] Based on a subjective score for muscling.
[3] Standard error of the mean for phenotype. Asterisks indicate a significant phenotype difference ($p<0.001$).

Table IV.2 Mean[1] metabolic rate ($kJ/kg^{0.75}/d$) by phenotype and age for carrier and double muscled (DM) bulls.

Phenotype[2]		Age		
Carrier	DM	1 yr	3 yr	SEM[3]
365.9	415.0*	423.7	357.2*	12.4

[1] Four animals per mean.
[2] Based on a subjective score for muscling.
[3] Overall standard error of the mean. Asterisk in each row within each major heading indicates a significant phenotype or age difference ($p<0.05$).

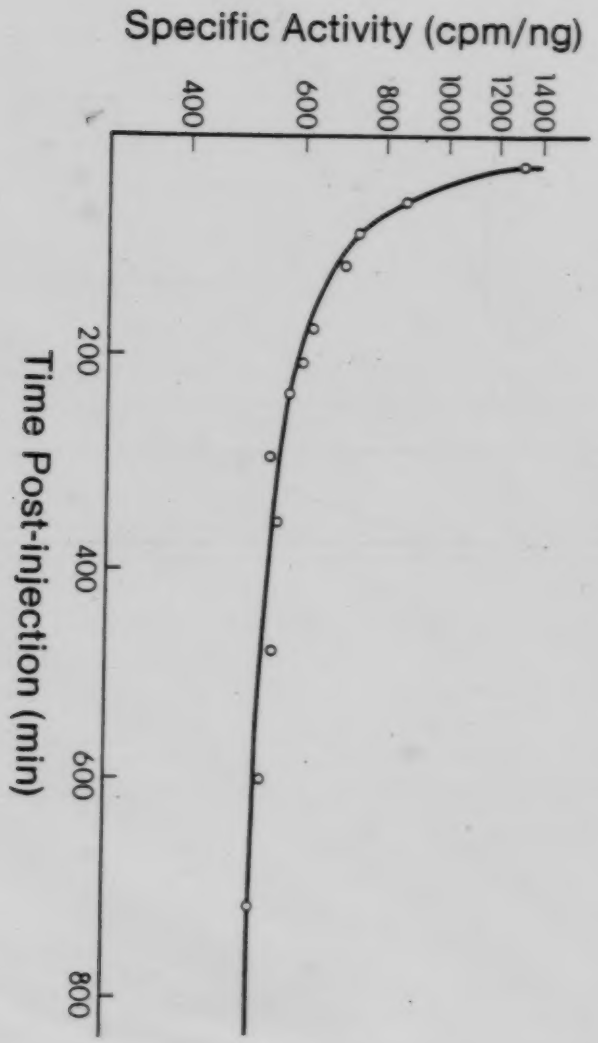

Figure IV.1 An example of the time course of serum specific activity in a double muscled bull following a single injection of ^{125}I-triiodothyronine.

V. REPRODUCTION IN DOUBLE MUSCLED COWS

A. Abstract

The reproductive performance of double muscled (DM) and phenotypically normal-to-moderate muscled (carrier) heifers and cows were studied. The calving records of carrier and DM heifers over a 4 yr period were compared. None of 8 DM heifers produced a live calf whereas all of 14 carrier heifers had live calves as a result of their exposure to a bull at 17 mo of age ($p<0.001$).

The endocrine and behavioural changes during the estrous cycles of 4 DM and 2 carrier cows from the DM herd were studied when penned with a DM bull. Blood samples were collected twice daily for 25 d and analyzed for estradiol-17β, progesterone and luteinizing hormone. All the cows except for 1 DM cow had normal hormone concentration patterns and behaviour at estrus, indicating that they had apparently normal estrous cycles. A normal muscled bull replaced the DM bull for a following 25 d period.

All of the cycling cows were diagnosed as being pregnant at approximately 4 mo following breeding and the carrier cows subsequently calved without assistance. One of the DM cows aborted while the other two required assistance with calving and one of these calves died a few days following birth. Visually the mammary glands of the DM cows which calved were smaller than those of the carrier cows. Plasma progesterone concentrations during the last 6 wk of

gestation were similar in carrier and DM cows, indicating that an imbalance in other synergistic hormones may be involved. It was concluded that the DM cows have an apparently normal estrous cycle and that anatomical and conformational characteristics of this cattle type may account for some of the associated reproductive problems.

B. Introduction

Muscular hypertrophy or the double muscled (DM) syndrome in cattle is frequently associated with characteristics which severely restrict animal production. DM cattle are more susceptible than normal cattle to stressors such as heat exposure (Halipre 1973), fasting (Holmes et al. 1973), exercise (Monin and Boccard 1974) and routine handling and transport (Holmes et al. 1973). The major disadvantage associated with this animal type, however, is the poor reproductive performance of the females. Vissac et al. (1974) have shown that puberty may be delayed, milk production is reduced and abnormal estrous cycles occur more often in DM than in normal cows. Dystocia, stillbirths and caesarian sections are relatively common in DM cows (Oliver and Cartwright 1968). Hanset and Jandrain (1979) have reported that more than 48% of the DM heifers and 25% of the DM cows in the Belgian Blue and White breed require caesarian section. Menissier et al. (1974) have suggested that the poor fertility of DM cows may be attributed to a defective sexual behaviour at estrus,

possibly arising from an endocrine disturbance. The objective of this study was to assess behavioural estrus and some associated endocrine changes in phenotypically normal and heavily muscled cows from a small DM herd.

C. Materials and Methods

All animals used in the following two studies were from a DM breed group maintained at The University of Alberta's Beef Research Ranch. The DM herd records indicate that reproductive problems are common. Externally, the reproductive organs of the most muscular cows in this herd appear infantile. All the calves born in the DM herd during a given year are generally half-siblings and are phenotypically scored (Basarab 1981) as either normal-to-moderate muscled (carrier) or extreme muscled (DM).

Study I

The calving records of carrier and DM heifers for a 4 yr period (1977-1981) were compared. Generally, all the heifers from the DM herd were bred to small statured "Pee Wee" (Berg 1980) bulls to reduce the incidence of calving difficulties. The statistical significance of the number of live calves born in each of the two phenotypes was determined by the Chi-Square test (Steel and Torrie 1980).

Study II

The endocrine and behavioural changes during the estrous cycles of three DM and two carrier 3-year old cows

and one DM 2-year old cow from the DM herd were studied. During the previous breeding seasons only one of four DM cows had a calf, while each of the carrier cows had two calves. All cows were penned together for a 25-day period with a DM herd bull which was a successful sire for the previous 2 breeding seasons. The animals were group fed 17 kg concentrate daily and grass hay was fed ad libitum. Blood samples were collected via jugular venipuncture (10 mL heparinized vacutainer tubes) at 0800 and 1800 h each day throughout the 25-day period. The plasma was removed and stored at -20°C until analysis. Visual signs of estrus were recorded during the daylight hours throughout this period. After the first 25-day period the DM bull was replaced by a larger normal bull for a second 25-day period.

A veterinarian diagnosed pregnancy by rectal palpation at approximately 4 mo gestation. Two pregnant carrier cows from the DM herd were added to the study at this time. Blood samples were collected once per wk for 6-to-10 wk before calving and the plasma was prepared and stored at -20°C until analysis.

Plasma progesterone concentration was measured in the morning samples of the first 25-day period by means of a radioimmunoassay kit (New England Nuclear, Boston, MA) and during gestation by a radioimmunoassay kit (Nuclear Medical Systems, Inc., Newport Beach, CA). Luteinizing hormone (LH) was measured in both the morning and afternoon samples by a radioimmunoassay kit (Diagnostic Products Corporation, Los

Angles, CA) and estradiol-17β was measured in the afternoon samples by the radioimmunoassay procedure of Rawlings et al. (1980). Commerical radioimmunoassay kits (Diagnostic Products Corporation, Los Angles, CA) were used to determine the concentrations of triiodothyronine (T_3) and thyroxine (T_4). Serum creatinine concentration was measured by means of a Beckman 2 Creatinine Analyzer (Fullerton, CA) in a blood sample obtained at the beginning of the study. Subcutaneous fat thickness was measured over the last rib at the time of pregnancy diagnosis by an ultrasonic scanner (Scanogram 722, Ithaca Inc., Ithaca, NY).

Statistical analysis between the carrier and DM cows was made using Student's t-test (Steel and Torrie 1980).

D. Results and Discussion

Average plasma thyroid hormone and creatinine concentrations and subcutaneous backfat thickness values for the carrier and DM cows are shown in Table V.1. DM cows tended ($P<0.1$) to have higher serum T_3 concentrations while no difference was observed for serum T_4 concentrations. Elevated concentrations of serum T_3 have been observed to be characteristic of DM cattle (Basarab 1981). The average serum creatinine concentration (2.3 mg/dL) for the DM cows tended ($P<0.1$) to be higher than that (1.4 mg/dL) for the carrier cows which agrees with the results of Ansay and Hanset (1979). A significantly lower ($P<0.05$) subcutaneous backfat thickness in the DM cows is also characteristic of

this animal type (Oliver and Cartwright 1968). The trend for higher concentrations of serum creatinine and thinner backfat reflect the leaner more muscular composition of the DM animals.

The DM herd breeding records (Table V.2) indicate that the DM heifers do not have calves as a result of their first exposure to a bull, which supports the observation of Vissac et al. (1974). To date, there have been only two heavily muscled DM cows from The University of Alberta's DM herd which have had calves which have lived to weaning age. Caesarian sections, stillbirths and high neonatal mortality are common for heavily muscled cows in this DM herd. These reproductive problems have been reported previously to be prevalent in other populations of DM cattle (Hanset and Jandrain 1979; Menissier et al. 1974; Vissac et al. 1974). Behavioural signs of estrus indicated that all cows except for one of the DM cows were cycling. In all of the cycling cows plasma progesterone concentrations decreased to levels approaching the limit of detection prior to estrus and then increased after estrus. Examples of the time course change in plasma progesterone concentrations for a carrier and a DM cow are shown in Figures V.1 and V.2, respectively. These observations are in agreement with the "typical" progesterone concentration pattern described by Sorensen (1979). In the non-cycling DM cow (Figure V.3) plasma progesterone concentrations did not follow the characteristic pattern and remained relatively low

throughout the 25-day sampling period.

Plasma concentrations of LH are not presented in the Figures as plasma sampling was not sufficiently frequent to characterize the size and duration of the LH peaks. Also, the assay was not specific to bovine LH consequently relative changes in LH concentrations and not absolute concentrations were measured. In this study plasma LH concentrations were observed to rise abruptly on the day of estrus in all cows showing behavioural estrus. Schams et al. (1977) have observed that LH peaks have an average duration of 7.4 h during estrus and most frequently occur at either 0800 or 1400 h, which are the approximate times when blood samples were collected in this study. Plasma estradiol-17β concentrations were observed to peak the day preceeding or the day of estrus (see Figure V.1) which agrees with the observations of Dobson and Dean (1974). The above endocrine patterns in the cycling cows appears to follow the "idealized" estrous cycle described by Hafs et al. (1976).

Two of the cycling DM cows did not conceive at their first estrus as hormonal and behavioural events associated with estrus were recorded again 18 to 20 d later. For this reason the cows were exposed to a large normal bull during the second 25-day period. The possibility that the enlarged rump of the DM cows and the smaller stature of DM bulls may interfere with mating has been suggested by Oliver and Cartwright (1968). McKellar (1960) has speculated that the infantile external reproductive tracts of DM cows may also

contribute to difficult mating. Possibly, the lower reproductive performance of DM cattle may be due in part to anatomical and conformational characteristics of this cattle type.

All of the cycling cows were diagnosed as being pregnant by means of rectal palpation at approximately 4 mo following breeding. All of the carrier cows calved without assistance. One of the DM cows aborted while the other two required assistance with calving and one of these calves died a few days following birth which further supports the observations of Hanset and Jandrain (1979).

Milk production is less in DM cows and Vissac et al. (1974) concluded that a possible endocrine imbalance may be responsible for this reproductive characteristic. Visually, the mammary glands of the DM cows which calved were smaller than those of the carrier cows which suggests that their ability to produce milk was reduced. The time course change in plasma progesterone concentrations during the last 6 wk of gestation do indicate that plasma concentrations of progesterone are similar in carrier and in DM cows at this time (Figure V.4). Progesterone is only one of the hormones involved in mammary gland growth and development, and some other synergistic hormones include estrogens, growth hormone, glucocorticoids, prolactin and the gonadotropins (Schmidt 1971). Not only is the concentration of a given hormone and its relationship to other hormones in the circulation important for mammary gland growth, but also the

sensitivity of the target cells to that hormone must be considered (Fulkerson 1979). Double muscled cows may have an endocrine imbalance or an abnormal sensitivity in mammary gland tissue to a given hormone which may account for the reduced milk production in this cattle type.

Although the number of animals studied was limited, it was apparent that reproductive problems such as delayed fertility in heavily muscled cows, routine calving assistance and neonatal mortality are common in DM cattle from The University of Alberta's population. Similar findings have been reported for other populations. Carrier and heavily muscled DM cows display similar estrous cycles as indicated by behavioural and hormonal observations. Cycling DM cows are capable of fertilization and conception, but may be less capable of carrying the fetus to term than normal muscled or carrier cows from the DM herd. Anatomical and conformational characteristics of this cattle type may also account for some of the associated reproductive problems of DM cattle. Studies of other endocrine factors may provide insight into the physiological basis of the problem and may suggest a means of successfully managing reproduction in heavily muscled cattle from DM herds.

E. References

ANSAY, M. and HANSET. R. 1979. Anatomical, physiological and biochemical differences between conventional and double-muscled cattle in the Belgian Blue and White breed. Livest. Prod. Sci. 6: 5-13.

BERG, R.T. 1980. The University of Alberta Kinsella Ranch-The first twenty years. The 59th Annual Feeders's Day Report. The University of Alberta. pp 3-9.

BASARAB, J.A. 1981. Genetic and physiological characterization of the double-muscle syndrome in cattle PhD Thesis. The University of Alberta.

DOBSON, H. and DEAN, P.D.G. 1974. Radioimmunoassay of oestrone, oestradiol-17α and -17β in bovine plasma during the oestrous cycle and last stages of pregnancy. J. Endocr. 61: 479-486.

FULKERSON, W.J. 1979. *Hormonal control of lactation*. Eden Press. Westmount, Quebec.

HAFS, H.D., MANNS, J.G. and LAMMING, G.E. 1976. Synchronisation of oestrus and ovulation in cattle. In: *Principles of Cattle Production*. Edited by H. Swan and W.H. Broster. Butterworths, Toronto. pp 45-58.

HALIPRE. A. 1973. Etude du caractere culard. X--Sensibilite des bovins culards au stress thermique. Ann. Genet. Sel. anim. 5: 441-449.

HANSET, R. and JANDRAIN, M. 1979. Selection for double-muscling and calving difficulties. In: *Calving problems and early viability of the calf*. Edited by B. Hoffmann, I.L. Mason and J. Schmidt. Martinus Nijhoff Publishers; The Hague, Boston, London. pp 92-104.

HOLMES, J.H.G., ASHMORE, C.R. and ROBINSON, D.W. 1973. Effects of stress on cattle with hereditary muscular hypertrophy. J. Anim. Sci. 36: 684-694.

MCKELLAR, J.C. 1960. The occurrence of muscular hypertrophy in South Devon cattle. Vet. Record 72: 507-510.

MENISSIER, F., CHUPIN, D., CHEMINANT, E., FABRE, F. and FABRE, G.P. 1974. Fertilite induite sensibilite a la P.M.S.G. de femellles culardes. In: *First World Congress on Genetics Applied to Livestock Production*. Madrid, Spain. pp 81-98.

MONIN, G. and BOCCARD, R. 1974. Caracteristiques physiologiques respiratoires des bovins culards. Ann. Genet. Sel. anim. 6: 187-193.

RAWLINGS, N.C., WEIR, L., TODD, B., MANNS, J. and HYLAND, J.H. 1980. Some endocrine changes associated with the post-partum period of the suckling beef cow. J. Reprod. Fert. 60: 301-308.

OLIVER, W.M. and CARTWRIGHT, T.C. 1968. Double muscling in cattle. A review of expression, genetics, and economic implication. Tech. Rep. No. 12, Dep. of Anim. Sci., Texas A&M University, College Station, Tex.

SCHAMS, D., SCHALLENBERGER, E., HOFFMANN, B. and KARG, H. 1977. The oestrous cycle of the cow: hormonal parameters and time relationships concerning oestrus, ovulation, and electrical resistance of the vaginal mucus. Acta Endocrinologica 86: 180-192.

SCHMIDT, G.H. 1971. *Biology of Lactation*. W.H. Freeman and Company, U.S.

STEEL, R.G.D. and TORRIE, J.H. 1980. *Principles and Procedures of Statistics*. McGraw-Hill Book Co. Inc., New York, N.Y.

SORENSEN, A.M. 1979. *Animal Reproduction: Principles and Practices*. McGraw-Hill Book Company, Toronto.

VISSAC, B., PERREAU, B., MAULEON, P. and MENISSIER, F. 1974. Etude du caractere culard IX--Fertilite des femelles et aptitude maternelle. Ann. Genet. Sel. anim. 6: 35-48.

Table V.1 Mean physiological parameters for carrier and double muscles (DM) cows.

	Phenotype[1]		
	Carrier	DM	SEM[2]
Triiodothyronine (ng/dL)	79	100	7.1
Thyroxine (ug/dL)	3.4	3.8	0.6
Creatinine (mg/dL)	1.4	2.3	0.3
Back-fat thickness (mm)	6.4	3.6	0.3 *

[1] Based on a subjective score for muscling.
[2] Standard error of the mean. Asterisk in each row indicates a significant phenotype difference($p<0.05$).

Table V.2 The number of carrier and double muscled (DM) heifers from a DM herd which calved between the years 1977-1981.

	Phenotype[1]		
	Carrier	DM	
Number of heifers	14	8	
Number of live calves born[2]	14	0	***

[1] Based on a subjective score for muscling.
[2] Asterisks indicate a significant phenotype difference ($p<0.001$).

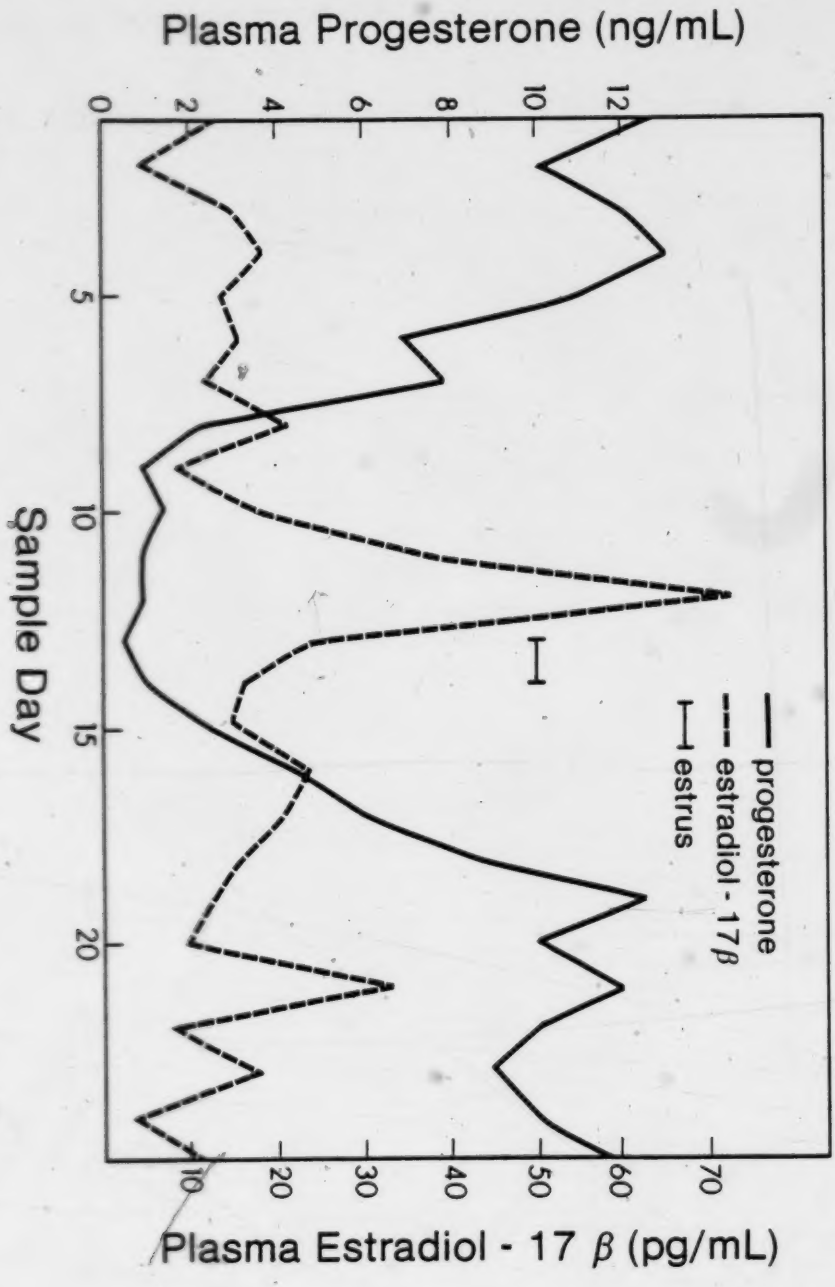

Figure V.1 Hormone concentration patterns in a cycling carrier cow.

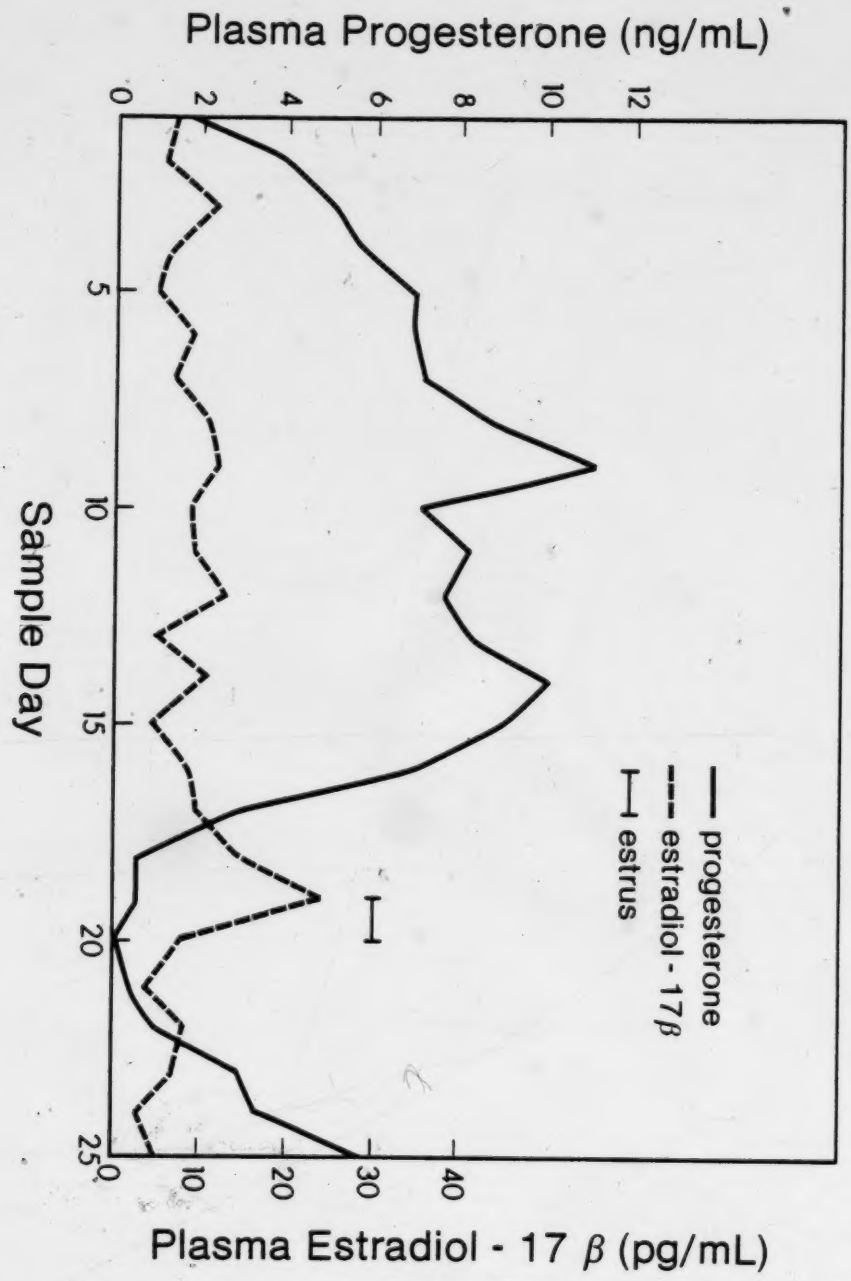

Figure V.2 Hormone concentration patterns in a cycling double muscled cow.

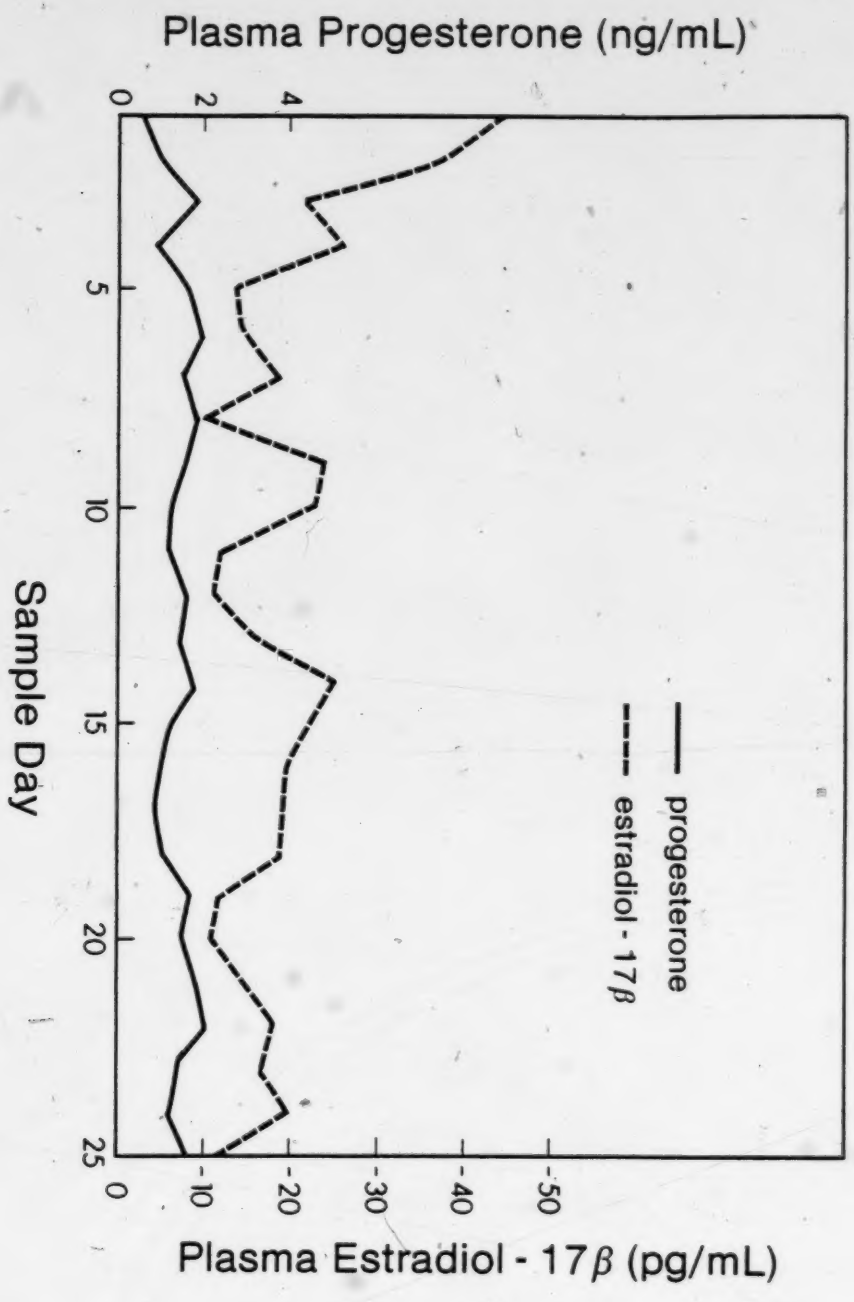

Figure V.3 Hormone concentration patterns in a non-cycling double muscled cow.

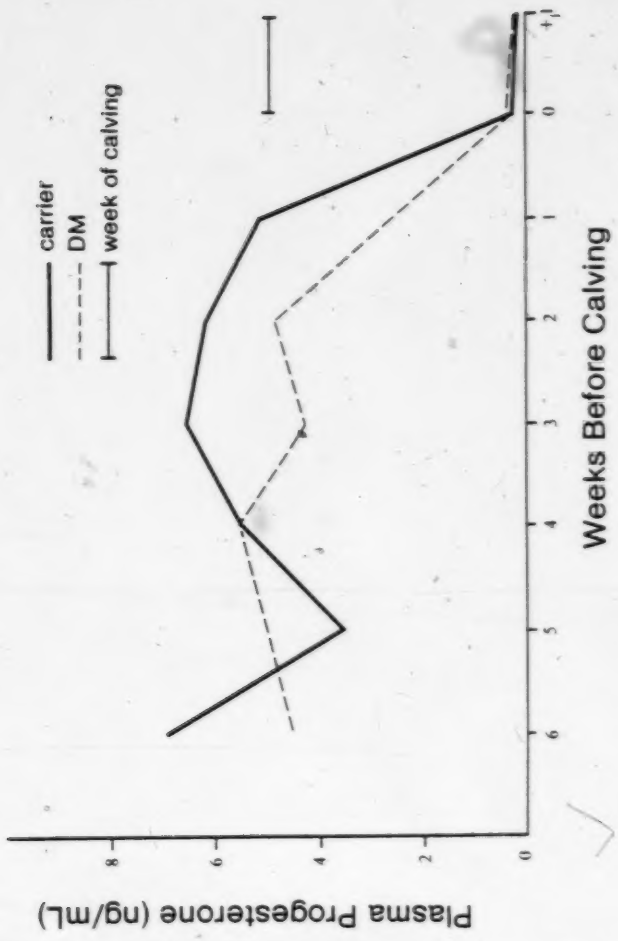

Figure V.4 Average plasma progesterone concentration during the last six weeks of gestation in carrier and double muscled cows.

VI. RESPONSE OF DOUBLE MUSCLED CATTLE TO HALOTHANE

A. Abstract

Halothane anaesthetic was administered to acheive stage III plane 2 anaesthesia (anaesthesia) in phenotypically normal-to-moderate muscled (carrier) and double muscled (DM) cattle. In the first study three DM and seven carrier 5 mo old bull calves were grouped and forced to run at 20 km/h around an alleyway for 2.4 km. Blood samples were collected before the exercise and 24 h post-exercise when the halothane was administered. Two DM calves were unable to complete the exercise so it was discontinued for these animals. Plasma creatinine was higher ($p<0.001$) in the DM calves and creatine phosphokinase activity was elevated post-exercise for both animal types ($p<0.05$). Anaesthesia was maintained for 5 min, 24 h post-exercise and no significant effect was observed for rectal temperature and neither skeletal muscle tremors nor rigidity were observed.

In the second study four DM and four carrier 9 mo old calves had anaesthesia maintained for 30 min by means of halothane inhalation. Neither muscle tremors nor muscle rigidity occurred after exposure to halothane while heart rate was elevated for both animal types ($p<0.001$). Rectal temperature of the DM cattle decreased only slightly from an initial mean of 38.9°C to 38.7°C after the 30 min period of anaesthesia, whereas the initial rectal temperature of the carrier cattle was 39.5°C and decreased to 38.8°C ($p<0.001$).

This difference in rectal temperature response between the phenotypes may reflect the decreased ability of DM cattle to lose body heat or to an elevated heat production of this cattle type.

In the third study a 4 mo old bull calf had anaesthesia induced by Nembutal and maintained by halothane inhalation for 100 min. There were no signs of halothane sensitivity as indicated by rectal temperature, arterial pH, or by venous lactic acid, adrenaline and noradrenaline concentrations. It was concluded that halothane is an apparently safe anaesthetic for routine veterinary and experimental use in stress susceptible DM cattle.

B. Introduction

Double muscled (DM) cattle have some similarities to stress susceptible (SS) swine. Both of these animal types have enlarged muscles, reduced body fat and are more stress susceptible as compared to normal animals of their species (Ashmore 1974). The spectrum of muscle fiber types in their enlarged muscles are similar for both animal types and excess pre-slaughter stress can result in poor quality carcasses (Ashmore 1974). Furthermore, relatively fragile erythrocytes have been reported in both SS swine (Cheah and Cheah 1979) and DM cattle (Basarab et al. 1980). The metabolic rate is relatively higher in SS swine (Williams et al. 1977) and DM cattle (see Chapter IV) as compared to normal animals of their species. Another metabolic

similarity is the increased turnover of triiodothyronine in both SS swine (Marple et al. 1977) and DM cattle (see Chapter IV).

Halothane, a fluorinated hydrocarbon anaesthetic, causes a condition known as malignant hyperthermia in SS swine (Britt 1972). The predominant clinical symptoms for malignant hyperthermia in SS swine are muscular rigidity, hyperthermia, tachycardia, hyperventillation, severe metabolic acidosis, elevated levels of some serum metabolites and blotchy cutaneous cynanosis (Williams 1977). The induction of muscle rigidity in pigs by halothane appears to be a reliable indicator of SS swine (Webb and Jordan 1978). Due to the numerous similarities between SS swine and DM cattle, the object of this study was to evaluate the usefulness of halothane as an anaesthetic for routine research and veterinary use in DM cattle.

C. Materials and Methods

All animals used in the following series of studies were from the double muscled herd maintained at The University of Alberta's Beef Research Ranch. Cattle within the DM breed group were phenotypically categorized (Basarab 1981) as either extreme in muscling (DM) or normal-to-moderate in muscling (carrier). In all of the studies outlined below, the animals were anaesthetized so as to achieve stage III plane 2 anaesthesia. Most routine surgical procedures requiring anaesthesia can be performed

at this level of anaesthesia.

Study I

Three DM and seven carrier 5 mo old bull calves from the DM herd were separated from their dams. A jugular vein blood sample was obtained by venipuncture and the plasma obtained following centrifugation was stored at -20°C. After collection of blood samples the calves were grouped and forced to run at 20 km/h around an alleyway for 2.4 km.

Approximately 24 h later blood samples were collected and processed as above, after which the calves were exposed to halothane. A mask was held over the face of an animal while it was restrained in a cattle squeeze. Anaesthesia was induced by the inhalation of 5% halothane in oxygen via a vaporizer and a semi-closed absorber system (Ayerst, Model VML5, Fraser Sweatman Ltd., Scarborough, Ont.) without prior administration of tranquilizers. Stage III plane 2 anaesthesia was maintained for 5 min. Rectal temperature was measured by a rectal probe and telethermometer (Yellow Springs Instruments Co., Inc., Yellow Springs, OH). and muscle condition was monitored by manually moving and palpating the hind limbs.

The plasma samples were analyzed for thyroxine (T_4) and triiodothyronine (T_3) concentrations by commerical radioimmunoassay kits (Diagnostic Products Corporation, Los Angles, CA). Creatine phosphokinase (CPK) activity was measued in the plasma samples by a colourometric method (Sigma No. 520, St. Louis, MO) and plasma creatinine

concentration was determined by a Beckman Creatinine Analyzer (Fullerton, CA). The data were analyzed by analysis of variance (Steel and Torrie 1980)

Study II

Four DM and four carrier 9 mo old calves from the double muscled herd were used in this study. Each animal had been exposed to halothane during one or more previous surgical manipulations. Individual animals were haltered and anaesthesia was induced by inhalation of 4 to 5% halothane in oxygen without prior administration of tranquilizers. Stage III plane 2 anaesthesia was maintained for 30 min by means of inhalation of 3 to 5% halothane in oxygen. Throughout the study heart rate was determined by use of a stethescope, respiration rate was measured visually and rectal temperature was measured by a rectal probe and telethermometer (Yellow Springs Instruments Co., Inc., Yellow Springs, OH). The data were analyzed by analysis of variance (Steel and Torrie 1980).

Study III

A 4 mo old DM bull calf had anaesthesia induced by infusion of 25 mL of Nembutal (pentobarbital 50 mg/mL) by means of a jugular vein catheter. After approximately 100 min, stage III plane 2 anaesthesia was maintained by inhalation of 2% halothane in oxygen. The concentration of halothane was progressively decreased to 0.25% during the subsequent 100 min at which time the animal was allowed to breath room air.

Throughout the experimental period and for 30 min following halothane administration, physiological parameters were monitored and blood samples were collected. Heart rate was measured by ECG needle electrodes inserted through the animal's hide and an ECG recorder (Hewlett-Packard, Mississauga, Ont.). Respiration rate was monitored visually and rectal temperature was measured by a rectal probe and telethermometer (Yellow Springs Instruments Co., Inc., Yellow Springs, OH). Blood samples obtained via the jugular vein catheter were analyzed for lactic acid (Sigma No. 115-A, St. Louis, MO) and for plasma noradrenaline and adrenaline concentrations (Graham et al. 1981). Blood pH and pCO_2 were monitored by a blood gas analyzer (Instrumentation Laboratory pH/Blood Gas Analyzer 813, Lexington, MA) in samples obtained via a catheter inserted into a branch of the femoral artery.

D. Results and Discussion

The results of study I are presented in Table V.1. There were no significant differences due to phenotype or to the exercise for plasma T_3 or T_4 concentrations. Basarab (1981) has observed elevated serum T_3 concentrations in DM cattle compared to normal and carrier cattle, whereas Novakofski and Kauffman (1981) observed lower serum T_3 levels in DM cattle. Differences in the reported serum T_3 concentrations may reflect the influence of stress prior to blood sampling as the effect of both fasting and heat stress

resulted in a depression in serum T_3 concentration in DM bulls while the levels in carrier bulls remained relatively constant (see Chapter II). A more meaningful measure of thyroid hormone status may be obtained by kinetic studies (see Chapter IV). The significantly ($p<0.001$) elevated plasma creatinine concentration in the DM calves is a characteristic of this cattle type which has been observed by Ansay and Hanset (1979). There was a significant decrease ($p<0.05$) in plasma creatinine concentration for both phenotypes the day following the exercise.

A significant ($p<0.05$) increase in plasma CPK activity was observed the day following the exercise (Table VI.1). Bickhardt et al. (1977) reported that the measurement of plasma CPK activity the day following an exercise stress may be of value as a predictive test for identifying SS pigs. Since pigs are generally reared in confinement the CPK activity post-exercise appears to have some merit, but limitations of the test include the sampling site, the timing of the blood collection post-exercise and limitations such as muscle damage during handling (Sybesma and Eikelenboom 1978). During the forced exercise two of the heavily muscled DM calves were unable to keep up with the other calves and exhibited abnormal behaviour in that they attempted to run through a wire fence. Abnormal behaviour due to a possible lactic acid build-up in DM cattle has been reported by Holmes et al. (1972b). Also exercise can result in severe muscle damage in DM cattle (Holmes et al. 1972a),

so the exercise was discontinued for these 2 DM calves in order to minimize muscle damage. Due to the inability of DM cattle to complete an exercise of less than 2.4 km the possible predictive value of post-exercise plasma CPK activity is limited.

In study I all of the calves except for 1 DM calf reached stage III plane 2 anaethesia in 3 to 8 min after halothane exposure. After 20 min of halothane inhalation the DM calf which had not reached stage III plane 2 anaesthesia had the halothane anaesthetic discontinued. Rectal temperatures remained constant and neither skeletal muscle tremors nor rigidity were observed as a result of the halothane anaesthetic. The recovery of each animal following halothane anaesthesia occurred within a 4 to 13 min period of time and none of the animals displayed abnormal signs during the 24 h period following anaesthesia. Unlike the SS pigs (Eikelenboom and Minkema 1974), it would appear that a few minutes exposure to halothane as a predictive test can not be applied to the stress-susceptible DM cattle.

Similar results were observed in study II as neither muscle tremors nor muscle rigidity occurred after exposure to halothane. A significant ($p<0.001$) increase in heart rate for all animals from the initial mean of 74 beats/min to 108 beats/min after 30 min of stage III plane 2 anaesthesia was observed (Table VI.2). The respiratory rate for both phenotypes was not affected by the halothane exposure. A significant ($p<0.001$) interaction was observed for phenotype

by time of rectal temperature measurement. The rectal temperature of the DM cattle decreased only slightly from a mean of 38.9°C for the initial recording to 38.7°C after the 30 min period of stage III plane 2 anaethesia, whereas the initial rectal temperature of the carrier cattle was 39.5°C and decreased to 38.8°C ($p<0.001$). This difference in rectal temperature response between the phenotypes may reflect the decreased ability of DM cattle to lose body heat (Monin and Boccard 1974) or to an elevated heat production of this cattle type (see Chapter IV).

The results presented in Figure VI.1 demonstrate that halothane anaesthesia in a DM calf had a minimal influence on the physiological and blood chemistry parameters measured. The calf's skeletal muscles remained relaxed with no apparent signs of muscle rigidity. Undesirable responses similar to those indicative of maligant hyperthermia or halothane sensitivity in the SS swine did not develop. The calf did not develop metabolic acidosis during halothane inhalation as indicated by the constant lactic acid concentration of approximately 6 mg/mL blood. The decrease in blood pH and increase in blood pCO_2 during halothane inhalation was indicative of slight respiratory acidosis. Plasma concentrations of adrenaline and noradrenaline increased slightly during halothane inhalation but not to concentrations normally observed during severe animal stress.

Generally, both humans (Henschel and Locher 1977) and SS swine (Ashmore 1974) which develop malignant hyperthermia are relatively muscular and leaner than normal individuals of their species. Malignant hyperthermia has also been reported in a Greyhound dog (Bagshaw et al. 1978) and a thoroughbred colt (Klein 1975) which are lean animals and have excitable temperaments. The similarities between SS swine and DM cattle have been emphasized, but differences have been reported. The enlarged muscles of DM cattle are primarily due to an increased number of muscle fibers whereas SS swine have larger muscle fibers which are mainly responsible for their muscular hypertrophy (Swatland and Cassens 1974). Relatively severe reproductive problems are associated with the DM syndrome in cattle (Vissac et al. 1974) whereas only minor reproductive problems have been reported in SS swine (Howard and Smith 1977). The results of the present study indicate that the muscular and stress susceptible DM cattle do not develop any of the symptoms of malignant hyperthermia when exposed to halothane, unlike SS swine (Williams 1977).

In summary, DM and carrier cattle from The University of Alberta's herd responded in a similar manner to halothane anaesthesia. One difference however, was that the rectal temperature in DM cattle remained constant while the rectal temperature in carrier cattle decreased after 30 min of stage III plane 2 anaesthesia maintained by halothane. The difference in rectal temperature response may have been due

to either a lower rate of loss or due to an increased heat production in the DM cattle. Lactic acidosis did not occur in a DM calf after exposure to halothane and the skeletal muscles remained flaccid and tremors were not observed. Halothane is an apparently safe anaesthetic for routine veterinary and experimental use even in DM cattle from the population under study. There are numerous similarities between SS pigs and DM cattle, but susceptibility to halothane anaesthesia is apparently not one of them. The reaction to halothane is therefore unlikely to be of value as a predictive test for stress susceptibility in cattle as it is in SS swine which develop malignant hyperthermia.

E. References

ANSAY, M. and HANSET. R. 1979. Anatomical, physiological and biochemical differences between conventional and double-muscled cattle in the Belgian Blue and White breed. Livest. Prod. Sci. 6: 5-13.

ASHMORE, C. R. 1974. Phenotypic expression of muscle fiber types and some implications to meat quality. J. Anim. Sci. 38: 1158-1164.

BAGSHAW, R.J., COX, R.H., KNIGHT, D.H. and DETWEILLER, D.K. 1978. Malignant hyperthermia in a Greyhound. JAVMA 172: 61-62.

BASARAB, J.A. 1981. Genetic and physiological characterization of the double-muscled syndrome in cattle. PhD Thesis, The University of Alberta.

BASARAB, J.A., BERG, R.T. and THOMPSON, J.R. 1980. Erythrocyte fragility in "double-muscled" cattle. Can. J. Anim. Sci. 60: 869-876.

BRICKHARDT, K., FLOCK, D.K. and RICHER, L. 1977. Creatine-kinase (C.K.-test) as a selection criterion to estimate stress resistance and meat quality in pigs. Vet. Sci. Comm. 1: 225-232.

BRITT, B.A. 1972. Recent advances in malignant hyperthermia. Anesth. Analg. 51: 841-850.

CHEAH, K.S. and CHEAH, A.M. 1979. Mitochondrial calcium, erythrocyte fragility and porcine malignant hyperthermia. FEBS Letters 107: 265-268.

EIKELENBOOM, G. and MINKEMA, D. 1974. Prediction of pale, soft, exudative muscle with a non-lethal test for the halothane-induced porcine malignant hyperthermia syndrome. Tijdschr. Diergeneesk. 99: 421-426.

GRAHAM, A. D., CHRISTOPHERSON, R. J. and THOMPSON, J. R. 1981. Endocrine and metabolic changes in sheep

associated with acclimation to constant or intermittent cold exposure. Can. J. Anim. Sci. 61: 81-90.

HENSCHEL, E.O. and LOCHER, W.G. 1977. The Wausau story--Malignant hyperthermia in Wisconsin. In: *Malignant Hyperthermia: Current Concepts*. Edited by E.O. Henschel. Appleton-Century-Crofts. New York, N.Y. pp 3-7.

HOLMES, J. H. G., ASHMORE, C. R., ROBINSON, D. W., FINN, J. P. and O'DELL, J. 1972a. A condition resembling "Azoturia" in a "Double Muscled" heifer. Vet. Rec. 90: 625-630.

HOLMES, J. H. G., ROBINSON, D. W. and ASHMORE, C. R. 1972b. Blood lactic acid and behaviour in cattle with hereditary muscular hypertrophy. J. Anim. Sci. 35: 1011-1013.

HOWARD, A.N. and SMITH, W.C. 1977. A note on purebred performance of Belgian Pietrain pigs. Anim. Prod. 25: 225-258.

KLEIN, L.V. 1975. Case report: A hot horse. Vet. Anesth. 2: 41-42.

MARPLE, D.N., NACHREINER, R.F., PRITCHETT, J.F., MILES, R.J., BROWN, H.R. and NOE, L.S. 1977. Thyroid and saracoplasmic reticulum function in halothane-sensitive swine. J. Anim. Sci. 45: 1375-1381.

MONIN, G. and BOCCARD, R. 1974. Caracteristiques physiologiques respiratoires des bovins culards. Ann. Genet. Sel. anim. 6: 187-193.

NELSON, T.E. 1970. Porcine stress syndromes. In: *International Symposium on Malignant Hyperthermia*. Edited by R.A. Gordon, B.A. Britt, W. Kalow. Charles C. Thomas Publisher, USA. pp 191-197.

NOVAKOFSKI, J.E. and KAUFFMAN, R.G. 1981. Biological detection of heterozygosity for double muscling in cattle. II. Thyroid hormone concentrations. J. Anim. Sci. 52: 1437-1441.

STEEL, R.G.D. and TORRIE, J. H. 1980. *Principles and Procedures of Statistics.* McGraw-Hill Book Co. Inc., New York, N.Y.

SWATLAND, H.J. and CASSENS, R.G. 1974. The role of innervation in muscle development and function. J. Anim. Sci. 38: 1092-1102.

SYBESMA, W. and EIKELENBOOM, G. 1978. Methods of predicting pale, soft, exudative pork and their application in breeding programmes--a review. Meat. Sci. 2: 79-90.

VISSAC, B., PERREAU, B., MAULEON, P. and MENISSIER, F. 1974. Etude du caractère culard. IX--Fertile des femelles et aptitude maternelle. Ann. Genet. Sel. anim. 6: 35-48.

WEBB, A.J. and JORDAN, C.H.C. 1978. Halothane sensitivity as a field test for stress-susceptibility in the pig. Anim. Prod. 26: 157-168.

WILLIAMS, C.H. 1977. The development of an animal model for the fulminant hyperthermia porcine stress syndrome. In: *Malignant Hyperthermia: Current Concepts.* Edited by E.O. Henschel. Appleton-Century-Crofts, New York, N.Y. pp 117-140.

WILLIAMS, C.H., SHANKLIN, M.D., HEDRICK, H.B., MUHRER, M.E., STUBBS, D.H., KRAUSE, G.F., PAYNE, C.G., BENEDICT, J.D., HUTCHENSON, D.P., LASLEY, J.F. and TRUMAN, H.S. 1977. The fulminant hyperthermia-stress syndrome: genetic aspects, hemodynamic and metabolic measurements in susceptible and normal pigs. In: *The Second International Symposium on Malignant Hyperthermia.* Edited by J.A. Aldrete and B.A. Britt. Grune & Stratton Publishers, New York. pp 113-146.

Table VI.1 Mean[1] response of 5 month old bull calves from a double muscled herd to exercise and to halothane anaesthesia (Study I).

Response to Exercise[2]													Response to Anaesthesia[3]			
Thyroxine (ug/dL)			Triiodothyronine (ng/dL)			Creatine (mg/dL)			CPK (Sigma units/mL)			Rectal Temperature (°C)			
Day			Day			Day			Day			Time			
1	2	SEM[4]	1	2	SEM	1	2	SEM	1	2	SEM	I[5]	0	5	SEM
4.1	4.6	0.2	168	173	10.1	1.5	1.4	0.02*	11	19	2.3*	39.3	39.5	39.5	0.1
Phenotype[6]			Phenotype			Phenotype			Phenotype			Phenotype			
C	DM	SEM	C	DM	SEM	C	DM	SEM	C	DM	SEM	C	DM[7]		SEM
4.4	4.5	0.5	164	178	13.4	1.2	1.9	0.1***	14	19	2.9	39.6	39.3		0.3

[1] Based on 7 C and 3 DM calves.
[2] Plasma parameters were measured before (day 1) and 24 h after (day 2) a 2.4 km exercise at 20 km/h.
[3] Rectal temperature was measured when halothane was initially administered (I) and at the start (0) and end of a 5 minute period ot state III plane 2 anaesthesia maintained with halothane.
[4] Standard error of the mean. Asterisk(s)in each row within each major heading indicates a significant treatment or phenotype difference (* $p<0.05$, *** $p<0.001$).
[5] Rectal probe was changed after initial measurements.
[6] Based on a subjective score for muscling; Carrier (C), Double Muscled (DM).
[7] Stage III plane 2 anaesthesia was only obtained for 2 of the 3 DM calves.

Table VI.2 Mean[1] response of 9 month old calves from a double muscled herd to halothane anaesthesia[2] (Study II).

Heart Rate (bpm)						
Time				Phenotype[3]		
I	0	30	SEM[4]	C	DM	SEM
74	92	108	3.9***	85	97	5.5

Respiratory Rate (rpm)					
Time			Phenotype		
0	30	SEM	C	DM	SEM
28	26	2.1	29	25	1.2

Rectal Temperature (°C)						
Time				Phenotype		
I	0	30	SEM	C	DM	SEM
39.2	39.1	38.8	0.03***	39.2	38.8	0.3

[1] Based on 4 C and 4 DM calves.
[2] Heart rate and rectal temperature were measured when halothane was initially administered (I) and at the start (0) and end (30) of a 30 minute period of stage III plane 2 anaesthesia maintained with halothane. Respiratory rate was measured at 0 and 30 minutes only.
[3] Based on a subjective score for muscling; Carrier (C), Double Muscled (DM).
[4] Standard error of the mean. Asterisks within a row of a major heading indicate a significant treatment difference ($p<0.001$).

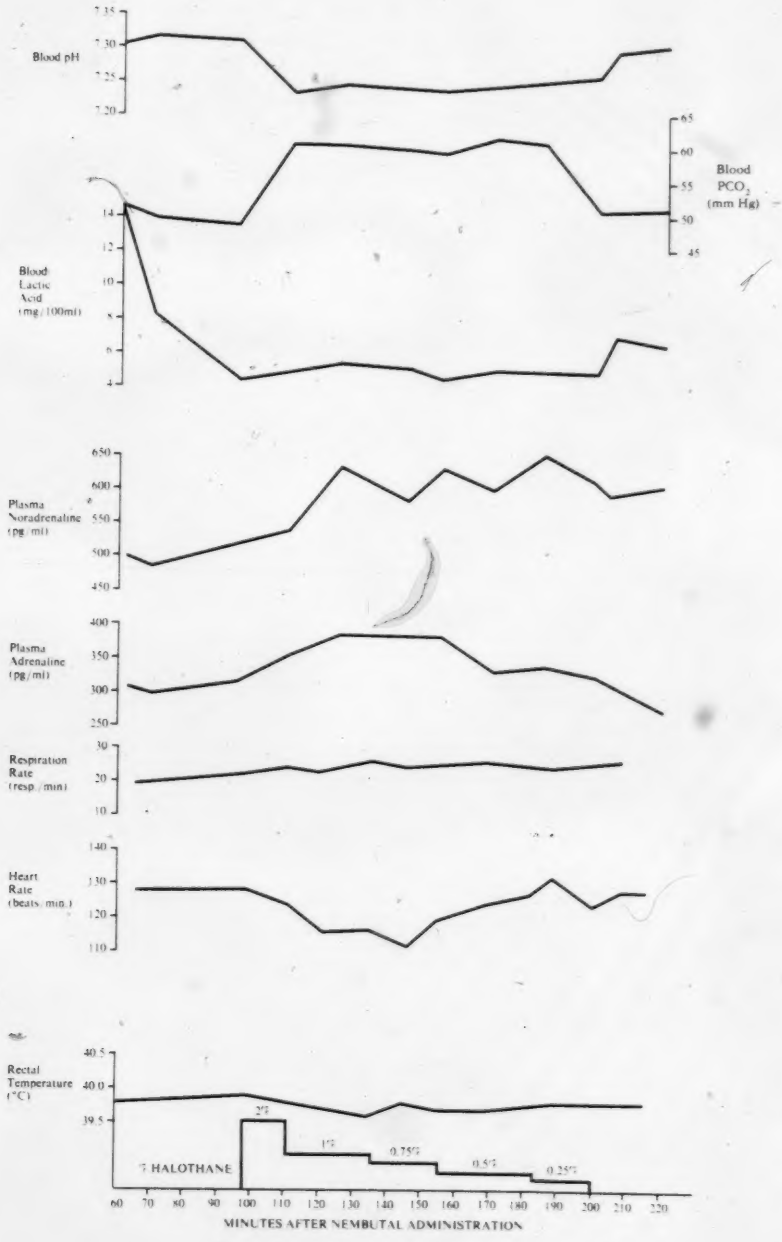

Figure VI.1 Response of a 4 month old double muscled bull calf to halothane anaesthesia.

GENERAL SUMMARY AND CONCLUSIONS

The objectives of this thesis were to study the metabolism and response of double muscled (DM) cattle to mild stressors and to identify some of the reproductive problems associated with this cattle type.

Metabolism and Effects of Mild Stress

Many authors have reported that DM cattle are very susceptible to relatively severe stressors. The investigations reported herein indicate that DM cattle are also susceptible to relatively mild stressors. Lactic acidosis has been reported to be a major consequence of stress in DM cattle. The effect of both fasting and a heat exposure did not result in an increased blood lactic acid concentration. Generally, for a high lactic acid concentration to be present an elevated metabolic activity of muscle tissue is required. In both fasting and heat exposure it is expected that metabolic activity of muscle tissue would be depressed, unlike that during exercise when muscle tissue metabolism is elevated and lactic acid production is high. Glucose metabolism, as indicated by plasma glucose kinetic parameters, in DM cattle was similar to carrier cattle. The smaller glucose pool size in DM cattle in both the fed and fasted states likely reflects, in part, the smaller size of the liver in this animal type.

Analysis of various metabolites and hormones, as well as metabolic rate has indicated that cattle displaying the trait for the DM syndrome respond metabolically and physiologically as though they are relatively hyperthyroid. The author emphasizes that this apparent hyperthyroid status of DM cattle is not likely the primary lesion in these animals, but may play a part in the resultant higher metabolism of this cattle type due to their lean and muscular composition.

Reproduction in DM Cattle

The major disadvantage of utilizing DM cattle in livestock production is their poor reproductive capabilities. Generally, DM heifers do not have calves as a result of their first breeding season. Observations of hormonal concentration patterns and behaviour at estrus in DM cows are indicative of apparently normal estrous cycles. DM cows are capable of fertilization and conception, but appear to be less capable of carrying the fetus to term. Anatomical and conformational characteristics of this cattle type account for some of the associated reproductive problems of DM cattle.

Future of DM Cattle

Cattle displaying the DM syndrome produce more lean meat than normal muscled cattle. Feed conversion is superior, rate of growth is higher, dressing percentage is

higher and meat obtained from DM cattle is more tender than that of conventional beef cattle. In many European countries where a premium is paid for lean meat, DM cattle production is profitable even though there are some serious production problems associated with this cattle type.

In North America the poor reproductive capabilities, poor neonatal viability and increased stress susceptibility of DM cattle limit their apparent value in beef cattle production. Animals which are heterozygous for the DM trait are called carriers and are phenotypically intermediate to normal muscled and DM cattle. Carrier cattle have superior carcass and meat qualities as compared with normal muscled cattle but do not have many of the associated production problems of DM cattle. Producers are being encouraged to raise carrier cattle as market animals in some production programs in order to exploit some of the qualities of the DM trait.

To successfully manage cattle displaying the DM syndrome more information is required about their metabolism and physiology. The primary cause of the DM syndrome is not known but it is most likely a result of either a neural and/or an endocrine disorder. The proposed general cell membrane defect may only be a reflection of the primary cause of the DM syndrome. To identify the primary genetic and biochemical cause of the DM sydrome it may be necessary to study the condition in utero when the developmental events are occurring.